

AN ABSTRACT OF THE THESIS OF

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Title: Advantages of Habitat Selection and Sexual Segregation in Mule and White-tailed Deer.

Signature redacted for privacy.

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I studied sexual segregation in mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus) in different environments and at different population densities to test the hypothesis that sexual segregation occurs in ungulates as the result of different reproductive strategies; females select habitat and behave in manners primarily designed to promote offspring survival, while adult males act primarily to maximize energy stores prior to the rut. Data collected for both species were consistent with this hypothesis. Mule deer segregated both socially and spatially. Compared to males, female mule deer used areas that were closer to water, supported superior browse species, and provided greater security for offspring from coyotes. Locally available resources enabled females to minimize movements, the apparent consequence of which was the depletion of forb biomass, the major diet class for both sexes. Males ranged further than females, a strategy that provided a diet high in forbs and high in quality. The occurrence of mixed-sex groups in highly productive areas suggested that males responded to forage availability and not females per se, and that the effects of localized grazing pressure by females may competitively exclude males from areas.

Sexual segregation was not maintained by intersexual aggression in either mule or white-tailed deer. White-

tailed deer segregated socially, but demonstrated broad spatial overlap. During the peak of segregation (June-October), male behaviors were consistent with a pre-rut energy saving and forage seeking strategy; males used larger areas and made longer short term movements than females, but were less active overall and were relatively more active at night. Females were less mobile and foraged in smaller areas than males, particularly during fawn rearing periods (June-October). I also tested the hypothesis that male white-tailed deer segregate and range widely to scout potential mates and rivals. Based upon comparisons of areas used by radio-collared males and females during the peak periods of segregation (June-September) with areas used during the rut, this hypothesis was rejected.

**Advantages of Habitat Selection and Sexual Segregation
in Mule and White-tailed Deer**

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ADVANTAGES OF HABITAT SELECTION AND SEXUAL SEGREGATION IN MULE AND WHITE-TAILED DEER

INTRODUCTION

In polygynous ungulates such as mule deer (Odocoileus hemionus) and white-tailed deer (Odocoileus virginianus), the selective pressures that determine whether individuals are reproductively successful operate differently on males and females. Consequently, behavioral patterns have evolved differently between the sexes. While these differences are most dramatic during the breeding season when males engage in combat over potential breeding partners, there are important behavioral differences that occur during nonbreeding periods as well. In fact, it is likely that what occurs during nonbreeding periods is ultimately far more important in terms of influencing reproductive success than the short expanse of time during which breeding actually occurs. This is especially true during spring and summer when female behaviors influence fawn survival the most, and when male behaviors determine growth and the accumulation of energy stores which directly influence both breeding success and the probability of avoiding winter starvation.

Among ungulates, and particularly in north temperate species, behaviors related to these differing reproductive objectives typically result in sexual segregation during nonbreeding periods. Sexual segregation describes the disassociation of conspecific adult males and females into separate social groups during nonbreeding periods, and is a nearly universal behavioral pattern among wild ungulates. In addition to the separation into separate social groups, the sexes may also use distinctly different geographical areas or habitat types. Although this behavior has been widely documented among wild ungulates

and is especially pronounced among north temperate cervids and bovids, the reasons for this behavior and the advantages it confers have only recently been studied in detail, and as yet remain a topic of debate.

This study examined sexual segregation among ungulates and included field studies of two species from different habitats and different population densities. Field studies were conducted on a low-density herd of mule deer living in the heterogeneous, high-desert of eastern Oregon, and on a high-density herd of white-tailed deer in a relatively homogenous, mesquite savannah in the south Texas coastal bend. Chapter 2 provides a review of the literature pertaining to sexual segregation in ungulates and examines a number of different hypotheses that have been proposed to explain this behavior. From available information on ungulate ecology, Chapter 2 develops arguments to reject most of these hypotheses and concludes by proposing that sexual segregation occurs among ungulates due to the different reproductive strategies of males and females. Chapters 3 and 4 present the results of field studies of mule deer from eastern Oregon. Chapter 3 compares male and female habitat from the perspective of why females select particular areas and the advantages they gain from these areas in terms of increasing offspring security. Chapter 4 also compares habitat and behavioral variables and addresses the reasons males avoid areas used by females. Chapter 5 is based on information collected during field studies of white-tailed deer in south Texas. Chapter 5 examines both habitat and behavior, and also tests a hypothesis proposed to explain segregation among white-tailed deer where males and females exhibit extensive distributional overlap.

SEXUAL SEGREGATION AMONG UNGULATES: A CRITIQUE

CHAPTER 2

Introduction

Sexual segregation is common among north temperate ungulates and has been investigated among a number of species including caribou (Rangifer tarandus; Jakimchuk et al., 1987), chamois (Rupicapra rupicapra; Shank, 1985), North American deer (Odocoileus spp.; McCullough, 1979, 1985; McCullough et al., 1989; Bowyer, 1984; Ordway and Krausman, 1986; Beier, 1987; Verme, 1988), elk (Cervus elaphus; Peek and Lovaas, 1968), red deer (Cervus elaphus; Watson and Staines, 1978; Staines et al., 1982; Clutton-Brock et al., 1982, 1987), pronghorn (Antilocapra americana; Kitchen, 1974), and bighorn sheep (Ovis canadensis; Geist and Petocz, 1977; Morgantini and Hudson, 1981; Shank, 1982; Gionfriddo and Krausman, 1986). Nonetheless, adaptive advantages of this behavior remain a matter of debate. Precipitated by the recent hypothesis related to antlerogenesis proposed by Verme (1988), this critique reviews existing hypotheses put forth to explain sexual segregation among ungulates and summarizes previous research as a basis to defend the view that sexual segregation occurs as a result of differing energetic and reproductive strategies.

Review of Current Hypotheses

Hypotheses proposed to explain sexual segregation include:

1. Altruistic departure by males from superior range to minimize competition with females, their young, and potential future offspring (Geist and Petocz, 1977; McCullough, 1979; Geist, 1982).
2. Predator avoidance by males exhausted from the rigors of reproduction (Geist and Bromley, 1978).
3. Minimization of sexually motivated aggression among males during periods when reproduction is not possible (Morgantini and Hudson, 1981).
4. Departure by males to relatively open habitats where male-dominance hierarchies can be maintained and risk of damage to antlers during antlerogenesis is reduced (Verme, 1988).
5. Optimization of forage resources by males and selection of habitat suitable for raising young by females (Geist, 1982; Bowyer, 1984; Clutton-Brock et al., 1987; Jakimchuk et al., 1987).

Implicit in the first hypothesis is group selection, *i.e.*, nonbreeding males willingly avoid areas with superior foraging opportunities to avoid competing with unrelated offspring. Among ungulates, breeding success is limited to those males that can gain or monopolize access to receptive females (Clutton-Brock et al., 1982; Berger, 1986). Because breeding opportunities are not equally distributed among males, nonbreeding males would gain nothing and lose much by segregating to areas with reduced foraging opportunities.

Segregation as an antipredator strategy (Geist and Bromley, 1978) was proposed to explain this behavior among males immediately following the rut and preceding antler

shedding. Geist and Bromley (1978) interpret the subsequent shedding of antlers as a form of female mimicry that enables males to rejoin females while minimizing the risk of being selectively preyed upon. This explanation fails to address segregation prior to the breeding period (Bowyer, 1984; Verme, 1988; McCullough et al., 1989) or among bovids and has been rebutted directly by Morgantini and Hudson (1981). Although the possibility exists that segregation may provide relief from predation in some situations, this has not been demonstrated. Adult male ungulates often occupy areas of greater predator density (Jakimchuk et al., 1987), and predation generally is higher upon adult males than upon adult females (see McCullough, 1979).

Hormonal control of reproduction is sharply seasonal among north temperate ungulates. To our knowledge, sexually motivated aggression among male ungulates during nonreproductive periods has not been reported. Even the proponents of this hypothesis (Morgantini and Hudson, 1981) failed to document an occurrence of such behavior. Avoidance of male-male aggression during nonreproductive periods is not likely the impetus for sexual segregation.

Verme (1988) recently hypothesized that male cervids, specifically white-tailed deer (Odocoileus virginianus), segregate to open areas to maintain visual contact so that hierarchical status can be assessed and danger of damage to antlers during antler growth minimized. Hierarchical status influences breeding success of male cervids (McCullough, 1979), and antler size and configuration influence dominance status among males and mate selection by females (Hirth, 1977; Kucera, 1978; Bubenik, 1983; Bowyer, 1986). Verme (1988) contended that males remaining in brushy habitat would be unable to maintain the visual contact necessary for evaluation of

hierarchical status while placing themselves at risk of antler damage. His hypothesis implies that cervids living in open habitats need not segregate, yet sexual segregation has been reported for mule deer (Odocoileus hemionus) in desert and shrub-steppe (Ordway and Krausman, 1986; Scarbrough and Krausman, 1988) and in meadows (Bowyer, 1984), for red deer in grass and moorlands (Clutton-Brock et al., 1982), and for barren-ground caribou in the arctic tundra (Jakimchuk et al., 1987).

As an alternative explanation to Verme's (1988) hypothesis, bachelor groups may form as a consequence of males seeking similar forage resources while increasing their individual security by feeding as a group (Hamilton, 1971; Berger, 1978). Furthermore, occurrence of solitary adult males during nonbreeding periods has been reported for white-tailed deer (Hirth, 1977), and a "dominant floater," (i.e., a mature buck with high social ranking that associates with different groups throughout the year and utilizes a large home range), has been reported for white-tailed deer by Brown (1974). Perhaps the most compelling argument against Verme's (1988) hypothesis is that the protection of antlers cannot be used to explain mechanisms responsible for sexual segregation in bovids. Verme (1988) attempted to fit a unique explanation for a single species when the behavior described is common among polygynous ungulates.

The hypothesis that males select habitat on the basis of foraging opportunities while females select habitat suitable for raising young is based upon energetics and the differing reproductive strategies that exist between sexes in polygynous ungulates. In general, both males and females are in a depleted energetic state when they leave winter range (Mautz, 1978). Forage and environmental conditions become appropriate for replenishing energy

reserves during spring and summer (Mautz, 1978), and it is during these periods that reproductive patterns differ most. Size and strength influence reproductive success among polygynous males (Clutton-Brock et al., 1982; Berger, 1986). Males grow and replenish fat reserves rapidly during summer (Wood et al., 1962). Maximizing opportunities to build muscle and accumulate energy reserves would, presumably, improve chances for acquiring mates. Successful females, on the other hand, may select habitats suitable for birthing, raising, and protecting young (Lent, 1974), even when this means compromising foraging opportunities (Geist, 1982; Jakimchuk et al., 1987).

Synopsis of Previous Research: Diet and Habitat Quality

As pointed out by Verme (1988), studies of diet and habitat quality have been inconclusive and at times confusing. I contend, however, that the absence of inconsistent results is an artifact of data collection and interpretation, and that fruitful avenues of research lie in the testing of hypotheses that consider aspects of forage availability and quality.

Analyses of rumen samples collected from segregated herds of red deer revealed that female diets were higher in nitrogen than male diets during winter, but not summer (Staines and Crisp, 1978; Staines et al., 1982). Although these results have been cited regularly as evidence that males segregate to poorer quality habitat, I suggest that alternate optimal strategies are being followed.

Supporting this contention were measures of total rumen nitrogen between males and females. Due to the larger rumen possessed by males, Staines et al. (1982) reported no difference between sexes in total rumen nitrogen per kg of metabolic bodyweight. They concluded that males filled up on lower quality heather (Calluna vulgaris) as an alternative to feeding on the heavily grazed grasslands and compensated for reduced forage protein by eating more.

Using fecal nitrogen as an index, Beier (1987) concluded that diets of female white-tailed deer were of generally higher quality than male diets over a 12-month period, with differences being largest in December and January. Analysis of rumen samples collected during January revealed that females consumed significantly more grass and less browse than males during winter. Although the utility of fecal nitrogen as an index of dietary quality has been questioned (Hobbs, 1987; Robbins et al., 1987; but see Leslie and Starkey, 1987), differences in

diet composition during January support Beier's conclusion that males are able to subsist on lower quality forage and do so in winter when higher quality food items are in low supply.

Both of these studies concluded that winter diets of females were superior in terms of forage protein. Crude protein and dry matter digestibility generally are selected as indices of forage quality because the nutritional value of a forage item for herbivores is related to its digestible protein and digestible-energy content (Schwartz and Hobbs, 1985), and measures of crude protein are strongly correlated with digestible protein (Dietz, 1970). During winter, however, protein may be less important to males than digestible energy due to reduced metabolic rates (Silver et al., 1969; Seal et al., 1972), a general cessation of growth (Wood et al., 1962), reduced forage consumption (Moen, 1973), and increased urea recycling in ruminants (Robbins et al., 1974). Shank (1982) measured species abundance and digestible energy of highly selected forages during a study of wintering bighorn sheep. Based on abundance and calculations of estimated digestible energy for the 2 most widely consumed forages, he concluded that rams used superior winter range.

Several studies have reported superior forage quality on female ranges based on physiographic characteristics such as elevation (Shank, 1985) and base soils (Watson and Staines, 1978). Although these factors may be correlated with nutritional content of forage, it is important to recognize that many environmental factors influence forage quality and these factors rarely act independently (Laycock and Price, 1970). Physiographic characteristics may be more important in providing security for neonates (Geist and Petocz, 1977; Leslie and Douglas, 1979;

Morgantini and Hudson, 1981; Gionfriddo and Krausman, 1986; Ordway and Krausman, 1986; Jakimchuk et al., 1987).

Nutritional quality may not be the only criteria upon which to judge feeding areas; availability of forage also may influence habitat selection. The larger rumen-to-body size ratio possessed by males may enable them to subsist on diets of lower quality (see Bowyer, 1984 and Beier, 1987).

During a study of southern mule deer, Bowyer (1984) measured percent cover and phenology of a preferred forage (Sisymbrium altissimum) during June. Percent cover was higher in female areas, but the overall availability of this forage did not differ between males and females when deer densities were considered. Bowyer (1984) determined that females used areas with forage in earlier phenological stages and nearer to sources of free water and suggested that segregation may be a result of water requirements by lactating females.

Ordway and Krausman (1986) measured composition and density of perennial vegetation in the spring and concluded that female desert mule deer preferred vegetative associations with superior foraging characteristics in all seasons; however, density of deer was not considered. Although annuals were not measured, Ordway and Krausman (1986) noticed that males modified range use in apparent response to forb abundance during spring and used both mountainous and nonmountainous vegetative associations throughout the year. Females were consistent in their selection of steeper slopes and mountainous vegetative associations.

Clutton-Brock et al. (1987) reported that segregation among red deer seems to be a result of passive competition from females for forage. Measurements of biomass and crude protein in grasslands revealed that foraging areas

used by males had significantly higher standing crops and higher average concentrations of crude protein than areas used by females. Observers also reported that use of short grasslands by males was less in areas where density of females was high, and that use of the long and short grasslands decreased as densities of females increased. Clutton-Brock et al. (1987) concluded that males avoid areas supporting low forage biomass and can be excluded from areas as a result of passive competition for forage from females.

Jakimchuk et al. (1987) reported that habitat selection by male caribou in central Alaska was in response to snow melt and plant phenology. During spring migration >70% of all male groups used relatively snow-free river valleys with newly emerging vegetation. Less than 10% of female groups used these areas; instead, females occupied areas with greater snow cover that were significantly farther from river valleys than expected and remained in these areas until after the calving period. Wolves (Canis lupus) and grizzly bears (Ursus arctos) commonly use river valleys for hunting and travel (see Jakimchuk et al., 1987). Based upon sightings of wolves (100%) and grizzly bears (75%) in river valleys, Jakimchuk et al. (1987) concluded that predator avoidance is a major factor influencing habitat selection by female caribou with calves. They also concluded that males use river valleys despite greater predator densities in efforts to replenish fat reserves in preparation for the next mating season.

Sexual segregation also has been reported in tropical ungulates. Prins (1989) estimated body condition of African buffalo bulls (Syncerus caffer) and determined that bulls lost condition when they associated in mixed herds and regained condition upon segregation. Prins

(1989) concluded that a periodic segregation was necessary for bulls to remain competitive for mates and caused bulls to enter a bachelor phase despite increased risk of predation. Risky male behavior for improved foraging opportunities also has been reported for Asian elephant (Elephus maximus) bulls, which raid crops much more frequently than mixed herds (Sukamar and Gadgil, 1988).

Summary

A review of sexual segregation among ungulates suggests that males and females select areas according to different criteria. I believe these criteria are a consequence of different reproductive strategies with females selecting areas suitable for raising offspring and males for maximizing body condition.

Site selection by females may be influenced by specific needs such as water requirements during lactation (Bowyer, 1984), presence of localized and persistent forage resources such as perennial browse (Ordway and Krausman, 1986), and predator avoidance (Jakimchuk et al., 1987). Predator avoidance may further be responsible for use of steep slopes or proximity to escape cover (Geist and Petocz, 1977; Leslie and Douglas, 1979; Gionfriddo and Krausman, 1986; Ordway and Krausman, 1986). As offspring become older and better able to escape predators, behavior and patterns of habitat use might be expected to change (Morgantini and Hudson, 1981).

During winter, protection of offspring may be of less concern than satisfying dietary needs due to the reproductive trade-off between caring for present young and future offspring (Trivers, 1972). Results from studies of winter diets suggest that females feed more selectively than males (Staines and Crisp, 1978; Staines et al., 1982; Beier, 1987), presumably due to their smaller size and the protein requirements of gestation (Moen, 1973). Males may have a greater need for digestible energy than for protein during winter, especially when rutting activities result in substantial weight loss (Moen, 1973). Results obtained by Shank (1982) for bighorn sheep and Staines et al. (1982) for red deer are consistent with this hypothesis.

Male mating success is influenced by body condition (Clutton-Brock et al., 1982; Prins, 1989), as is winter survival (Moen, 1973; Mautz, 1978). Replenishment of energy reserves should coincide with major growing seasons, and optimization of forage resources by males should be most evident during these periods as they prepare for rut. Optimal foraging by males may require avoidance of heavily grazed areas (Clutton-Brock et al., 1987) or the adoption of foraging patterns that exploit temporal resources of high quality (Ordway and Krausman, 1986). The importance of maximizing body condition for males apparently exceeds even increased risk of predation (Jakimchuk et al., 1987), and evidence provided by Prins (1989) strongly suggests that these risks are undertaken for reproductive motives.

SECURITY CONSTRAINTS AND GENDER DIFFERENCES IN
HABITAT USE BY MULE DEER
CHAPTER 3

Abstract

Habitat variables were measured at feeding sites used by male and female mule deer (Odocoileus hemionus hemionus) during May-October 1989 and 1990 at Hart Mountain National Antelope Refuge in southeastern Oregon. Female groups were found to use areas that were closer to water, more likely to support stands of palatable browse, and that provided greater security from coyotes than areas used by males, particularly when fawns were less than eight weeks old. Vegetation cover-types most preferred by female groups included mesic communities and bitterbrush (Pursia tridentata), while male groups were primarily observed in mountain big sagebrush (Artemisia tridentata vaseyana). Species richness and both horizontal and vertical cover of woody vegetation was greater at female sites, and females were more likely than males to use slopes $\geq 10^\circ$. Coyotes used slopes $< 10^\circ$ almost exclusively. Both genders used north and easterly aspects more than south and westerly. Differences in mean elevational distribution of males and females appeared to be an artifact of the distribution of water and cover-types preferred by females. The results of this study supported the hypothesis that, relative to males, female distribution was dependent upon resources that provided security for offspring.

Introduction

The selective pressures that mediate reproductive success in polygynous breeding systems operate differently on males and females (Clutton-Brock et al., 1988), particularly among species that sexually segregate and possess large intersexual differences in reproductive success. Polygynous ungulates generally conform to this scenario, and several hypotheses have been proposed to explain the advantages of sexual segregation in these animals (see Bleich, 1993; Main and Coblentz, 1990; Miquelle et al., 1992; for reviews).

Based on their review of previous studies, Main and Coblentz (1990) argued that sexual segregation occurs among polygynous ungulates as the result of different reproductive strategies; females occupy areas promoting offspring survival, while males exploit areas providing maximum forage intake. In polygynous ungulates, females assume complete responsibility for raising offspring and, therefore, their decisions related to offspring security and resource requirements are particularly critical when offspring are highly vulnerable (Clutton-Brock, 1991). This study compared habitat characteristics between areas used by males and females in a sexually segregated herd of Rocky Mountain mule deer (Odocoileus hemionus hemionus) in a mountainous region of southeastern Oregon. The objective of this study was to test the hypothesis that habitat use and distribution of female groups during fawning and fawn-rearing periods (May-October) would reflect behaviors that reduced the risk of predation to offspring, and that areas used by females could be differentiated from areas used by males on the basis of vegetation and physiographic characteristics that influenced offspring security.

Study Area

This study was conducted on approximately 14,000 ha of the 111,336 ha Hart Mountain National Antelope Refuge (HMNAR), located in the northern extreme of the Great Basin Desert (42°32'N, 119°40'W). The HMNAR study area was topographically diverse and included a mix of physiography, habitats, and elevations (ca. 1,500 - 2,100 m). The predominant geological feature at HMNAR is the 48.3 km fault block ridge that forms the sheer west face interspersed with rugged canyons. The west face rises approximately 1,000 m above the Warner Valley to an elevation of 2,458 m above sea level. Higher elevations are dominated by rolling plateaus with more gradual slopes and less rugged canyons descending eastward into foothill country (ca. 1,500 - 2,100 m) and beyond into the high-desert of the Catlow Valley (ca. 1,400 m elevation).

Vegetation at HMNAR has been classified as shrub-steppe (Franklin and Dyrness, 1973) and supports a diverse assemblage of browse dominated by mountain big sagebrush (Artemisia tridentata vaseyana) above 1,500 m. Mesic areas support stands of quaking aspen (Populus tremuloides), choke and bitter cherry (Prunus virginiana and P. emarginata), and snowbrush (Ceanothus velutinus). Western juniper (Juniperus occidentalis) and curlleaf mountain mahogany (Cercocarpus ledifolius) are present on the more xeric south slopes and ridge tops. The area is semi-arid, with annual precipitation occurring primarily as snowfall (50 year annual mean = 29 cm; USFWS, unpublished refuge records). Buck-only deer hunting is limited by permit and restricted to primitive weapons, all predators are protected, and only limited cattle grazing was allowed on portions of the refuge until 1990 when grazing was terminated.

Methods

Deer surveys were conducted along established routes during dawn and dusk approximately five days each week during 15 June-15 September 1988 (preliminary field season), 15 June-10 October 1989, and 1 May-15 September 1990. Analyses were restricted to data collected during the 1989 and 1990 field seasons. Routes and schedules were arranged to provide approximately equal effort among areas used by each sex. Deer groups (≥ 1 adult deer) represented the statistical unit in all analyses and were defined as male, female, or mixed-sex. Survey information was used to quantify deer use of vegetation cover-type, slope, aspect and elevation. Slope use was also recorded for coyotes (Canis latrans) during 1990. Locations of deer groups were also recorded during surveys with 4 ha grid overlays on 7.5 minute topographic maps. Location information was used to calculate the distance of each deer group to the nearest available water source. Seasonal time periods were categorized as: MJ (5/1-6/14), JJ (6/15-7/15), JA (7/16-8/15), AS (8/16-9/15), and OCT (10/1-10/10). Time periods were defined to roughly correspond with pre-fawning (MJ), parturition-postpartum (JJ), mid-summer (JA), late-summer (AS), and pre-rut (OCT) periods, respectively.

The study area was mapped according to seven vegetation cover-types (Table III.1.). Cover-types were defined by the Soil Conservation Service (J. Kinzle, U.S. Dep. Agric., Soil Conserv. Serv., unpubl. data), and reflected the dominant or distinguishing vegetative components. Riparian areas were classified by cover-type. Aspen-dominated riparian zones and snowy-north-complex communities (snowpockets) were defined as mesic areas. Vegetative cover-types were identified for the study area

from color infrared aerial photographs (National High Altitude Photography Program), ground-truthed, and transferred onto 7.5 minute topographic maps with zoom transfer scope overlays. Total area covered by each cover-type was calculated to ± 2 ha.

Log-linear models ($P < 0.05$) were used to test for differences in use of cover-types between years, among seasonal time periods, and among deer group-types (Sokal and Rohlf, 1981). Preference-avoidance of cover-types was statistically tested with G-tests according to the method of Neu et al. (1974) and Byers et al. (1984). Relative preference indices (RPI) were calculated as percent use divided by percent availability for each cover-type, and calculated separately for each group-type and seasonal time period.

Slope use was recorded in degrees and classified as (<10 , $10-25$, and $>25^\circ$). Aspects were categorized as either North and East (N-E) or South and West (S-W) due to the mesic and xeric characteristics of these aspects. Data were summarized as observation frequencies and analyzed with G-tests and log-linear analyses to test whether differences existed between years and among group-types for slope and aspect use. Contingency tables were used to test for differences in slope and aspect use during seasonal time periods when log-linear models revealed complete interaction effects (Sokal and Rohlf, 1981:749).

Analysis of variance (ANOVA) and Scheffe multiple range tests were used to test for differences between years and among group-types and within group-types among seasonal time periods in elevation, distance from water, horizontal and vertical shrub cover, and shrub species richness. Statgraphics^R (STSC) statistical software package was used for analyses.

Table III.1. Descriptions of cover-types at Hart Mountain National Antelope Refuge, labels reflect the dominant vegetation characteristic of each community.

Cover-type Label	Community Description
Mountain Big Sagebrush (MBS)	Dominant species is MBS (<u>A. t. tridentata</u>) with bunchgrass understory dominated by fescue (<u>Festuca</u> spp.) and mixed annual and perennial forbs.
Bitterbrush (BIT)	Dominant species are MBS and BIT (<u>Purshia tridentata</u>). Snowberry (<u>Symphoricarpos</u> spp.), rabbitbrush (<u>Chrysothamnus</u> spp.) common, with mixed understory dominated by needle grass (<u>Stipa</u> spp.).
Mesic Communities (MESIC)	Snow pocket communities located on north and east aspects dominated by snowbrush (<u>Ceanothus velutinus</u>), quaking aspen (<u>P. tremuloides</u>), or cherry (<u>Prunus</u> spp.) with mixed forb and grass understory. Riparian aspen communities also in this category.
Grassland (GRASS)	Grasslands, areas disturbed by fire, and meadows. Common species include bottle brush squirrel tail (<u>Sitanion hystrix</u>), cheat grass (<u>Bromus tectorum</u>), bluegrass (<u>Poa</u> spp.), and sedges (<u>Carex</u> spp.).
Pine/Juniper/Mountain Mahogany	Sites characterized by stands of ponderosa pine (<u>Pinus ponderosa</u>), western juniper (<u>Juniperus occidentalis</u>), or curlleaf mountain mahogany (<u>Cercocarpus ledifolius</u>).
Low Sagebrush	Shallow soils dominated by low sagebrush (<u>Artemisia arbuscula</u>) with bluegrass and Idaho fescue (<u>F. idahoensis</u>) common.
Other	All cover-types not fitting the above descriptions.

Elevations were recorded to the nearest 20 m with 7.5 minute topographic maps. Water sources were located with infrared aerial photographs and a thorough search of the study area during 1988-1990 and were monitored for availability twice each month during July-September 1990. Linear distances from deer groups to the nearest available water sources (± 200 m) were determined using Universal Transverse Mercator (UTM) coordinates (Grubb and Eakle, 1988). Distance data were square-root transformed prior to analysis.

Shrub species richness, horizontal cover, and vertical cover were measured at morning feeding sites for all group-types during June-September 1989 and 1990. Three 30 m transects were established at feeding sites using a stratified random approach (Pieper, 1978); species richness was quantified by direct counts (Peet, 1974), and horizontal shrub cover was measured for each species by line intercept (Canfield, 1941; Pieper, 1978). Vertical shrub cover was measured as percent cover in 0.5 m vertical intervals with a cover pole (Griffith and Youtie, 1988). Measurements were taken at each transect from four ordinal directions at a distance of 15 m (with eye-level at 1 m). Vertical cover data were arcsine square-root transformed prior to analysis (Sokal and Rohlf, 1981).

Results

Survey information was collected from 1,687 female, 492 male, and 165 mixed-sex deer groups during May-October 1989 and 1990 ($n \geq 1$ deer/group). Analysis of cover-type use was restricted to four cover-types plus a pooled "other" category because these four (MBS, MESIC, BIT, and GRASS; Table III.1.) included 95.5% of all observations and covered 71% of the study area. MBS was the dominant cover-type and encompassed 51% of the study area. BIT, MESIC, GRASS, and "other" cover-types constituted 6, 5, 9, and 29% of the study area, respectively. Cover-types differed among deer group-types, but did not differ between years, so years were pooled ($\chi^2 = 10.13$, $P = 0.12$). Cover-types were used significantly different from expected based on availability (Table III.2.). All group-types used MESIC cover-types more and "other" cover-types less than expected. Males preferred MBS, while females avoided this cover-type, and mixed-sex groups used it in proportion to availability. Females were the only group that used BIT preferentially, and all group-types used GRASS proportional to availability.

Seasonal RPI values failed to reveal any temporal pattern in preference of cover-types by male groups (Fig. III.1a.), but female groups demonstrated distinct seasonal cover-type preference (Fig. III.1b.). Female groups increased use of MESIC cover-types during the parturition-postpartum (JJ) period and then gradually decreased their use of MESIC as summer progressed, with an increase in the use of BIT and GRASS cover-types. Although mixed-sex groups were represented by small sample sizes, the data suggested that this group preferred MESIC cover-types during all periods and BIT during the late summer and pre-rut period (AS-OCT).

Figure III.1a. and 1b. Relative preference index ($RPI = \% \text{ use} / \% \text{ availability}$) for major cover-types by groups of adult (a) male and (b) female mule deer during May-October 1989 and 1990. RPI values >1 indicate preferential use. Total observations for each group and time period in parentheses.

Figure III.1.(a) Male Groups

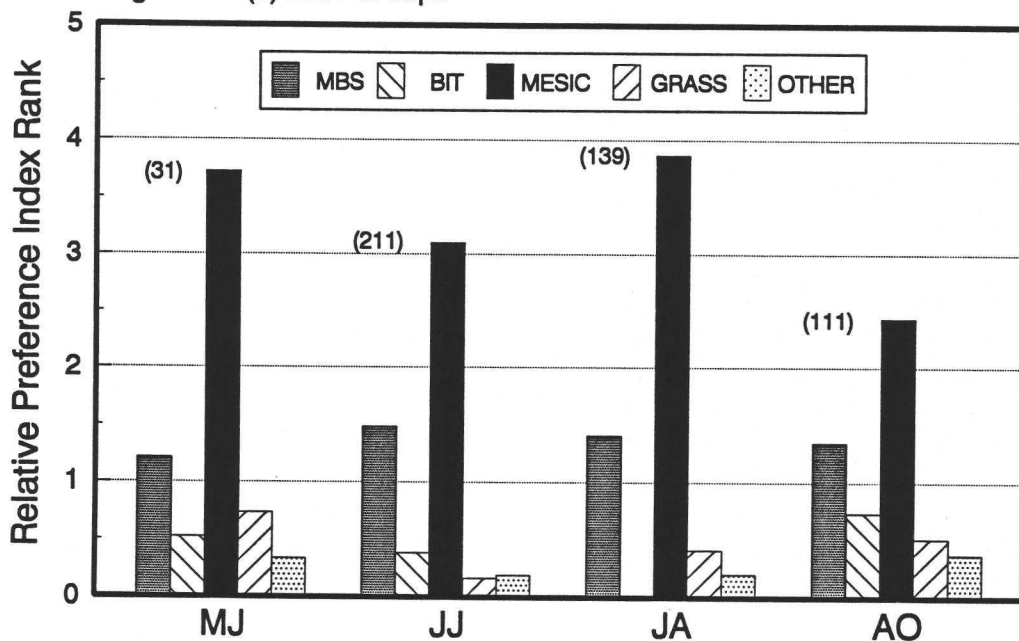


Figure III.1.(b) Female Groups

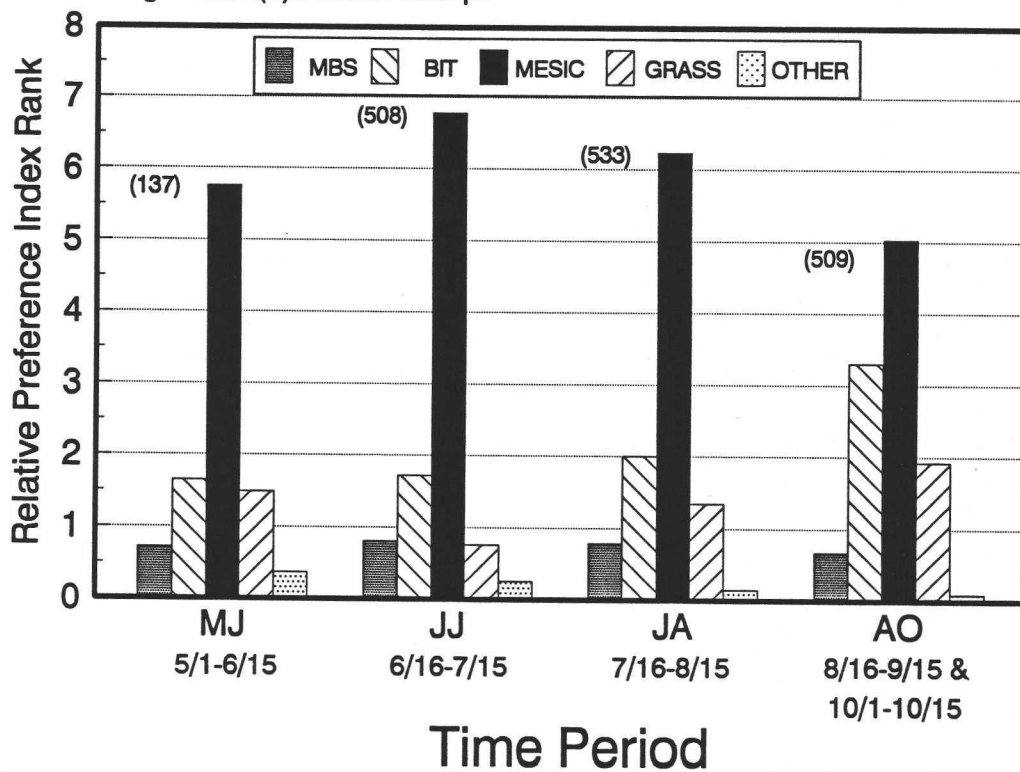


Table III.2. Use of major cover-types¹ (preference/avoidance)² during 1989 and 1990 by male, female, and mixed-sex deer groups. Asterisks indicate use is significantly different ($P < 0.05$) than expected based upon availability; associated + or - indicates direction of departure (greater or lesser use, respectively).

Group-type	n	G	P	Vegetative Cover-type				
				MBS	MESIC	BIT	GRASS	OTHER
MALE:	492	277	<0.001	*+	*+	NS	NS	*-
FEMALE:	1,687	1,745	<0.001	*-	*+	*+	NS	*-
MIXED:	165	128	<0.001	NS	*+	NS	NS	*-
Total cover (%):				50.3	5.2	6.2	8.8	29.5

¹See Table III.1. for descriptions of cover-types.

²Analyzed using G-statistic according to methods of Neu et al. (1974) and Byers et al. (1984).

Slope use did not differ ($P > 0.05$) between years for males and females so data were pooled. Slope use by mixed-sex groups differed significantly ($G = 7.44$, $P < 0.05$) between years and was eliminated from further analyses. Males, females, and coyotes used slopes differently ($G = 88.91$, $P < 0.001$; Fig. III.2.). Coyotes used slopes $<10^\circ$ almost exclusively, while male groups used all slope types. Female groups used slopes $\geq 10^\circ$ more than males ($G = 36.09$, $P < 0.001$) and coyotes ($G = 49.64$, $P < 0.001$). Only females demonstrated seasonal patterns in slope use ($X^2 = 66.59$, $P < 0.0001$), sharply increasing the use of steeper slopes during JJ, with a gradual decrease in the use of slopes $\geq 10^\circ$ as the summer progressed (Fig. III.3.).

Aspect use differed among group-types ($P < 0.05$), although all group-types used N-E aspects most ($X^2 = 2.25$, $P = 0.32$; Fig. III.4.). Males and females differed during JJ ($X^2 = 21.7$, $P < 0.0001$) and JA ($X^2 = 3.69$, $P = 0.05$).

Figure III.2. Percent slope use by gradient class for groups of adult male and female mule deer during May-October 1989 and 1990, and coyotes during 1990. Total observations in parentheses.

Figure III.3. Slope use by groups of adult female mule deer during May-October 1989 and 1990. Values in parentheses represent total observations during each time period.

Figure III.4. Percent use of north and east aspects by adult male and female groups during May-October 1989 and 1990. Total observations (all aspects) in parentheses.

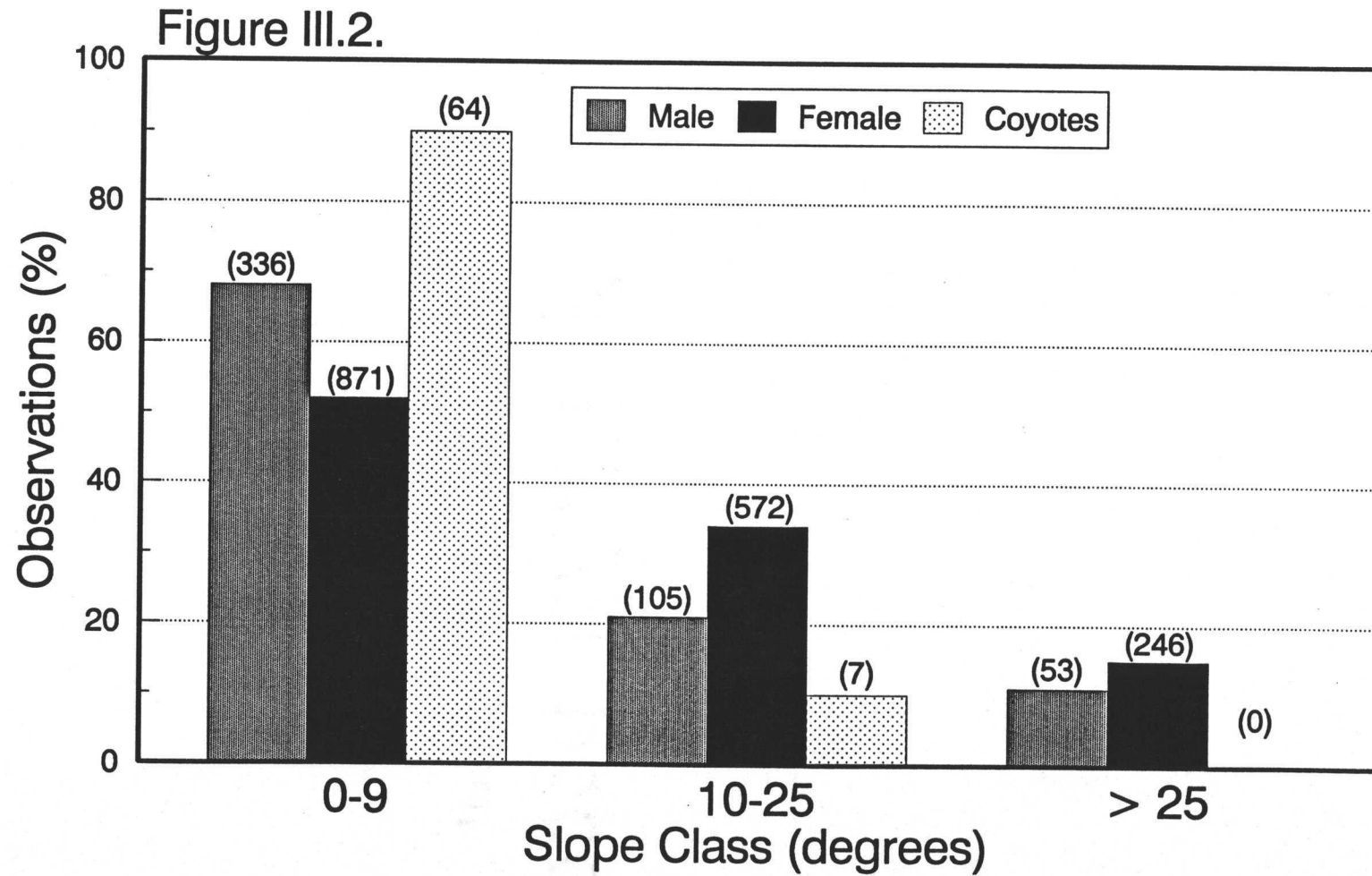
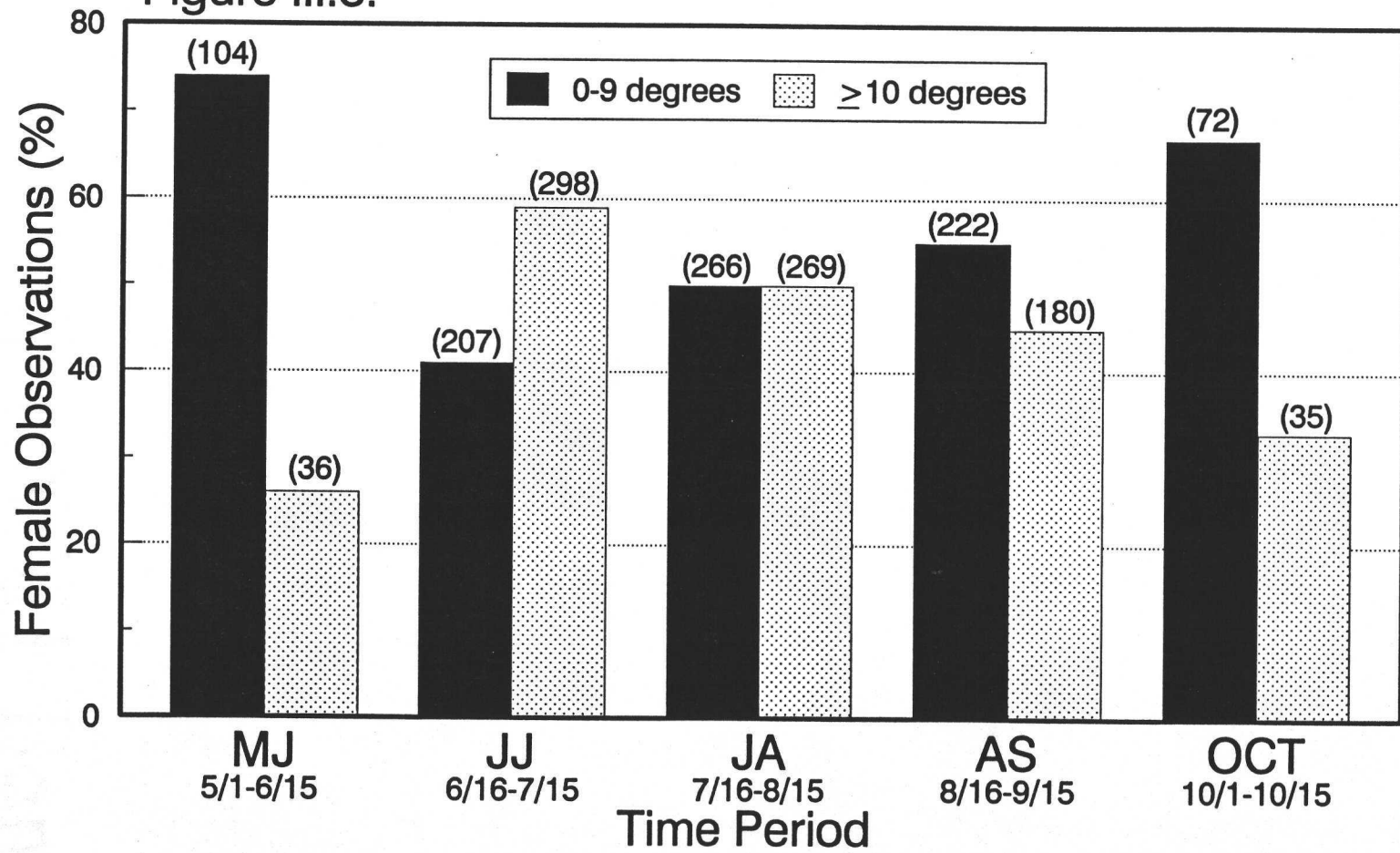
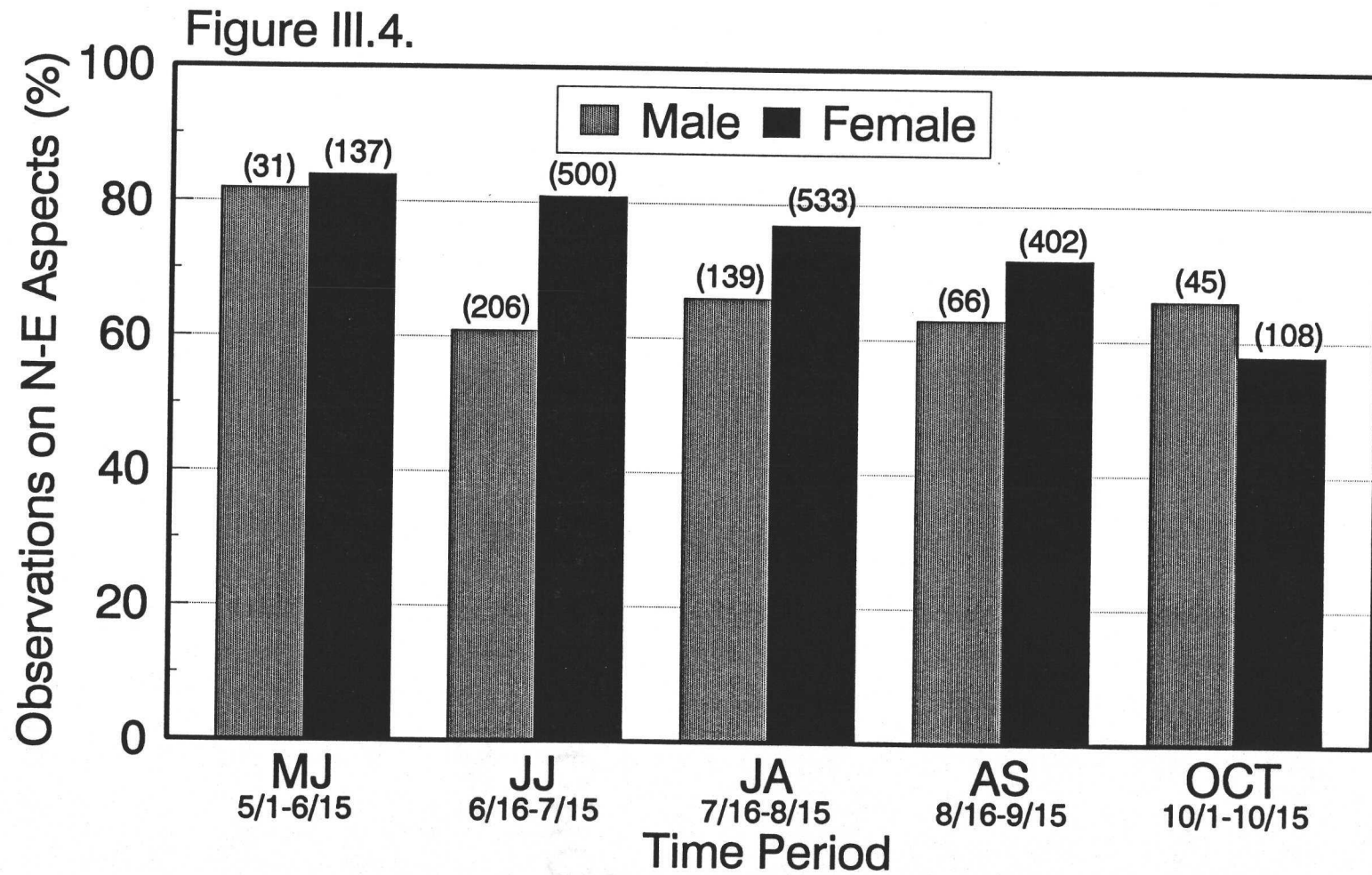


Figure III.3.





Females increased use of S-W aspects as summer progressed. No pattern was evident among male groups with the exception that N-E aspects were used the most during MJ and the least during OCT (Fig. III.4.).

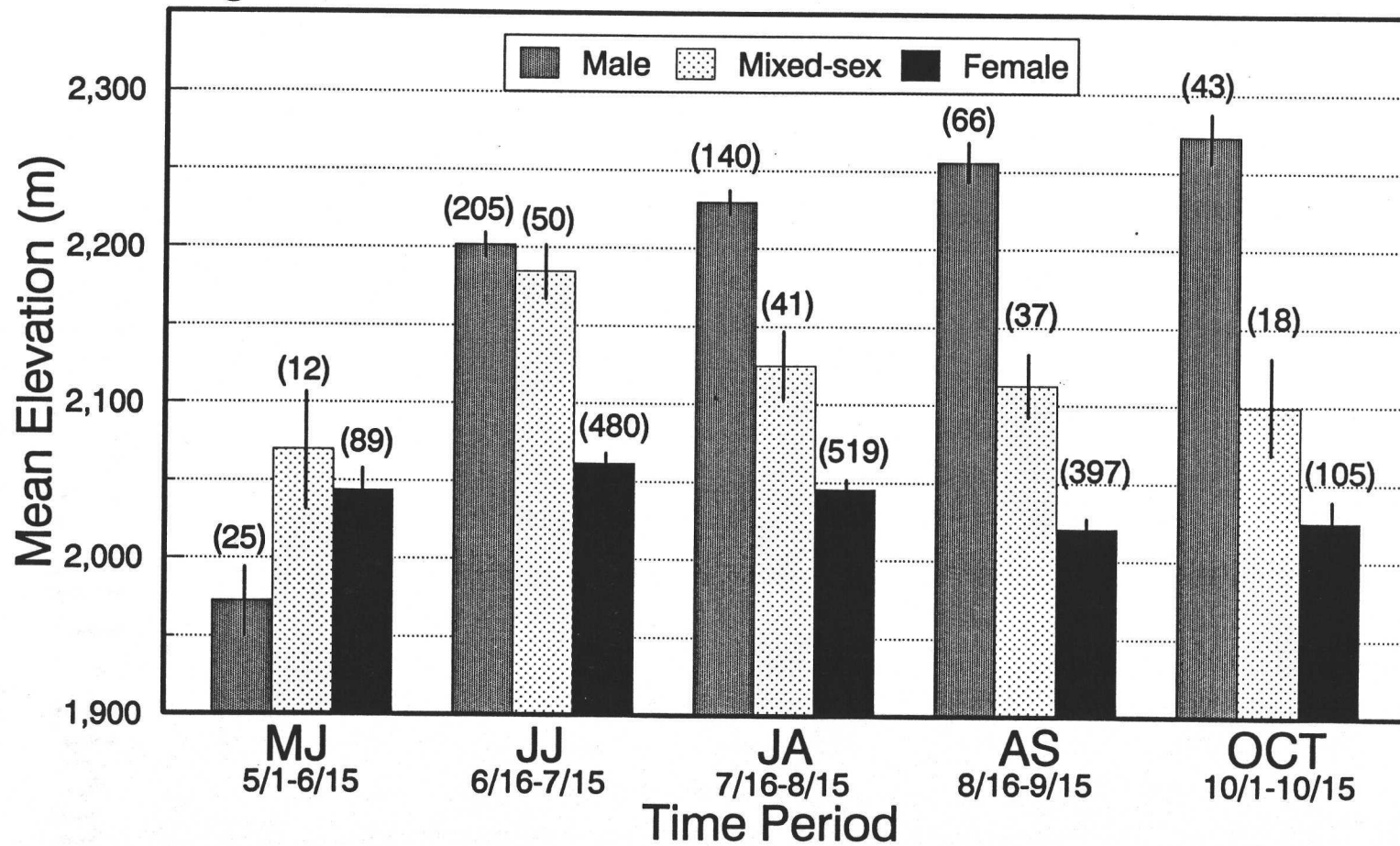
Significant differences were observed in elevational distribution among group-types ($F = 315.5$, $P < 0.0001$) and time periods ($F = 7.87$, $P < 0.0001$), but not between years ($F = 2.92$, $P = 0.09$). Female groups used the lowest mean elevations, male groups used the highest, and mixed-sex groups were typically found at intermediate elevations. Although the mean elevation of group-types differed, the range of elevations used by group-types were similar (Table III.3.). Temporally, group-types demonstrated differences in elevational patterns. The highest average elevations used by female groups coincided with the parturition-postpartum period (JJ), male groups followed a trend toward the use of higher elevations as summer progressed (Fig. III.5.). Mixed-sex groups occurred primarily at lower elevations during MJ when both males and females were still arriving from winter range and during the pre-rut period (OCT) when males were beginning to reappear in areas used by females.

Table III.3. Mean elevation and elevational range used by male, female, and mixed-sex deer groups during 1989 and 1990. Statistical comparisons determined by 95% Scheffe multiple range tests; nonaligned asterisks represent statistical differences among group-types at $P < 0.05$.

Group-type	n	Mean Elev. (m)	SE	Scheffe Tests	Elev. Range (m)	
					Max.	Min.
MALE:	479	2,199	6.4	*	2,440	1,815
FEMALE:	1,590	2,035	3.9	*	2,410	1,710
MIXED:	158	2,126	10.3	*	2,410	1,815

Figure III.5. Mean elevations (with SE) used by adult male, mixed-sex, and female mule deer groups during May-October 1989 and 1990. Values in parentheses represent total observations by group-type during each time period.

Figure III.5.



Ephemeral water sources typically disappeared in June and water was restricted to permanent sources by July. Proximity to water was similar during July-September ($F = 0.405$, $P = 0.531$) and differed by group-types ($F = 23.64$, $P < 0.0001$). Female groups were observed significantly closer to water than mixed-sex or male groups (Fig. III.6.), and mixed-sex groups were observed significantly closer to water than male groups. Although mean distance from water was greater for female groups without fawns than for females with fawns, these differences were not significant and were likely confounded by difficulties in detecting fawns. Male deer were often seen long distances (>3 km) from known water sources.

Shrub species richness differed significantly at feeding sites among group-types ($F = 8.56$, $P = 0.0004$), but not between years ($F = 0.46$, $P = 0.504$), nor among time periods ($F = 1.37$, $P = 0.26$). Female feeding sites had a significantly greater ($P < 0.05$) average number of shrub species ($\bar{X} = 3.2$, $SE = 0.14$) than either male ($\bar{X} = 2.4$, $SE = 0.14$) or mixed-sex ($\bar{X} = 2.56$, $SE = 0.22$) sites. Dominant species composition at feeding sites (measured as linear cover), also varied among group-types and reflected the characteristics of the vegetation communities that male, female, and mixed-sex groups typically used (Table III.4.).

Mean horizontal shrub cover at feeding sites was significantly different among group-types ($F = 3.82$, $P = 0.025$) but not between years ($F = 0.94$, $P = 0.345$), so years were pooled. Average shrub cover was greatest at female feeding sites and lowest at male sites; mixed-sex sites did not differ significantly from either male or female sites (Table III.5.). Shrub cover was significantly less during AS at female feeding sites ($F =$

4.23, $P = 0.021$), but did not vary seasonally at male feeding sites ($F = 0.40$, $P = 0.671$; Fig. III.7.).

Table III.4. Species composition (mean % cover) and summer forage quality rating¹ of dominant browse at male, female, and mixed-sex feeding sites during June-September 1989 and 1990.

Browse	Forage Quality	Mean Percent Cover		
		Male	Female	Mixed-sex
Aspen (<i>P. tremuloides</i>)	G	3.2	6.6	2.9
Snowbrush (<i>C. velutinus</i>)	G	10.5	36.0	2.1
Bitterbrush (<i>P. tridentata</i>)	G	0.1	14.6	<0.1
Snowberry (<i>S. albus</i>)	G	1.4	7.6	7.2
Wild Cherry (<i>Prunus</i> spp.)	G ²	<0.1	5.0	14.8
Mountain Big Sagebrush (<i>A. t. vaseyana</i>)	P/F	71.5	21.5	64.8
Rabbitbrush (<i>Chrysothamnus</i> spp.)	P	4.9	7.3	4.9
Other		8.4	1.4	3.4

¹P = poor, F = fair, G = good, and E = excellent (Leckenby et al., 1982; Roche, 1983).

²*Prunus* may be not be good until late summer (Robinette, 1966).

Table III.5. Mean horizontal shrub cover at male, female, and mixed-sex feeding sites ($\bar{n}$ = sites) during 1989 and 1990. Statistical comparisons determined by 95% Scheffe multiple range tests; nonaligned asterisks represent statistical differences among group-types at $P < 0.05$.

Group-type	$\bar{n}$	Mean shrub cover			Scheffe Tests
		%	cm ¹	SE	
MALE:	45	20.1	599	43	*
FEMALE:	46	24.6	757	42	*
MIXED:	18	22.0	620	67	**

¹Values represent mean cover per 30 m transect.

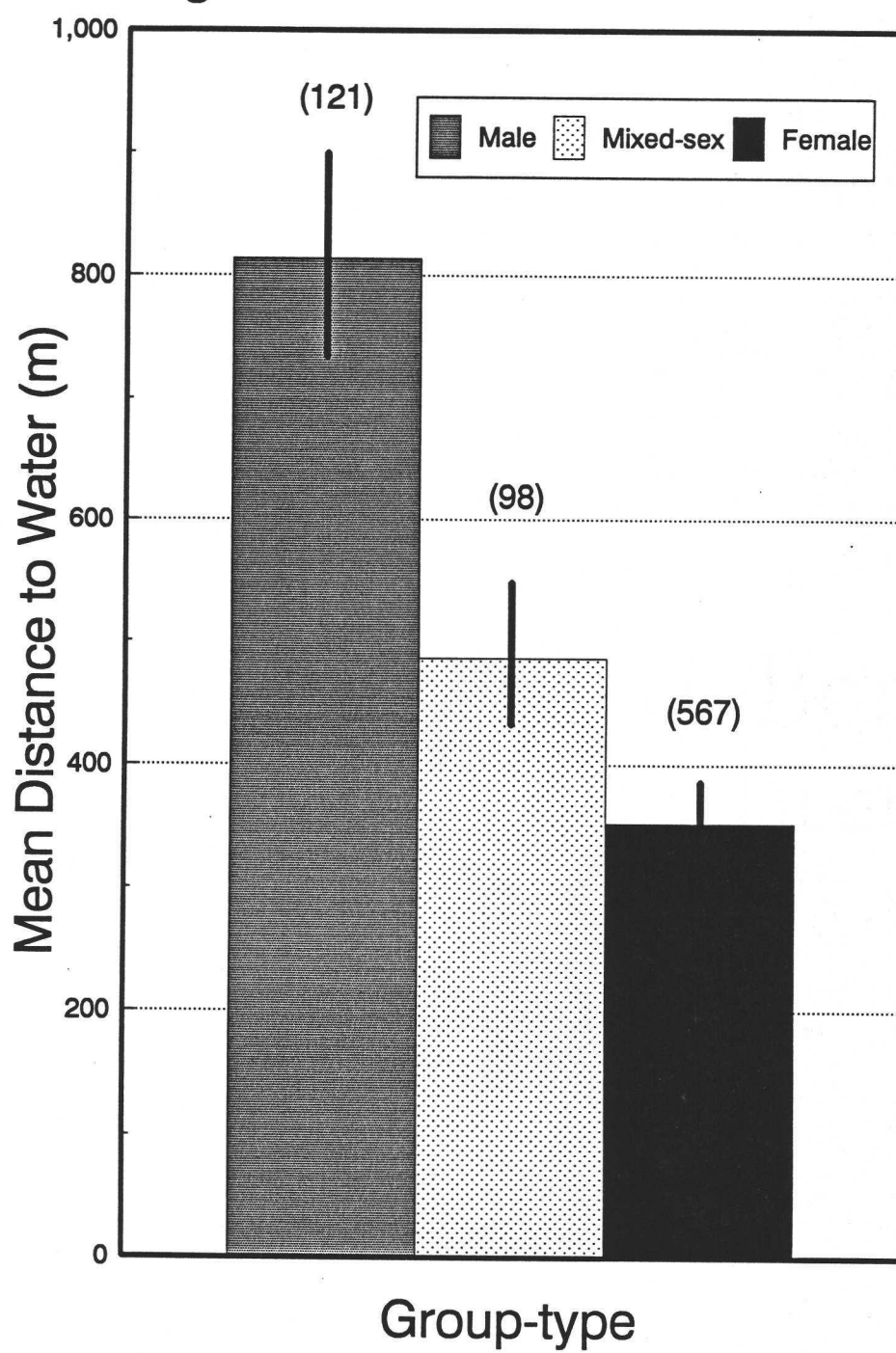
In addition to greater horizontal shrub cover, female feeding sites also had significantly greater vertical cover above 0.5 m than found at male sites, although cover below 0.5 m was similar ($F = 2.06$, $P = 0.129$). Analysis of vertical intervals above 0.5 m revealed consistent differences among group-types (Fig. III.8.), so these were combined and the average cover (0.5-2.0 m) was analyzed. Significant differences were found among group-types ($F = 5.96$, $P = 0.003$); vertical cover was significantly higher at female than male sites, and mixed-sex sites were intermediate. No seasonal differences (JJ, JA, AS) were found in the amount of vertical cover at feeding sites above 0.5 m ($F = 1.62$, $P = 0.201$) for any group-type. However, comparisons among MESIC, GRASS, and combined MBS-BIT cover-types revealed that vertical cover above 0.5 m differed significantly among these cover-types at female sites ($F = 24.38$, $P < 0.0001$; MBS-BIT > MESIC > GRASS), but not at male sites ($F = 1.91$, $P = 0.169$).

Figure III.6. Mean distance to water (with SE) for adult male, female, and mixed-sex groups of mule deer during July-September 1990. Values in parentheses represent total observations by group-type.

Figure III.7. Mean horizontal shrub cover (with SE) at feeding sites used by adult male, mixed-sex, and female mule deer during June-September 1989 and 1990. Values in parentheses represent total number of feeding sites by group-type and time period.

Figure III.8. Mean vertical cover (with SE) by 0.5 m interval at adult male, mixed-sex, and female mule deer feeding sites during June-September 1989 and 1990. Values in legend represent total feeding sites by group-type.

Figure III.6.



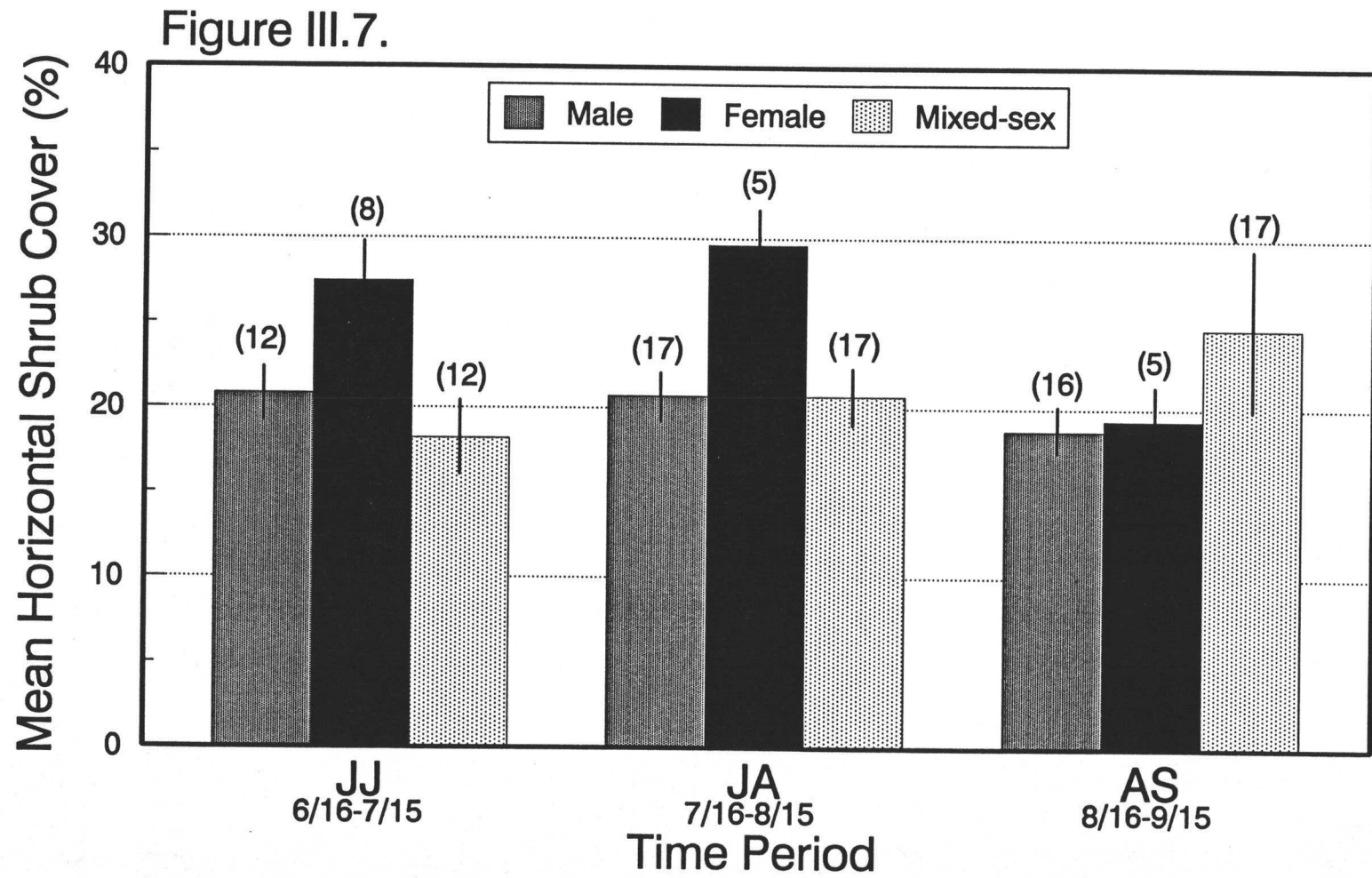
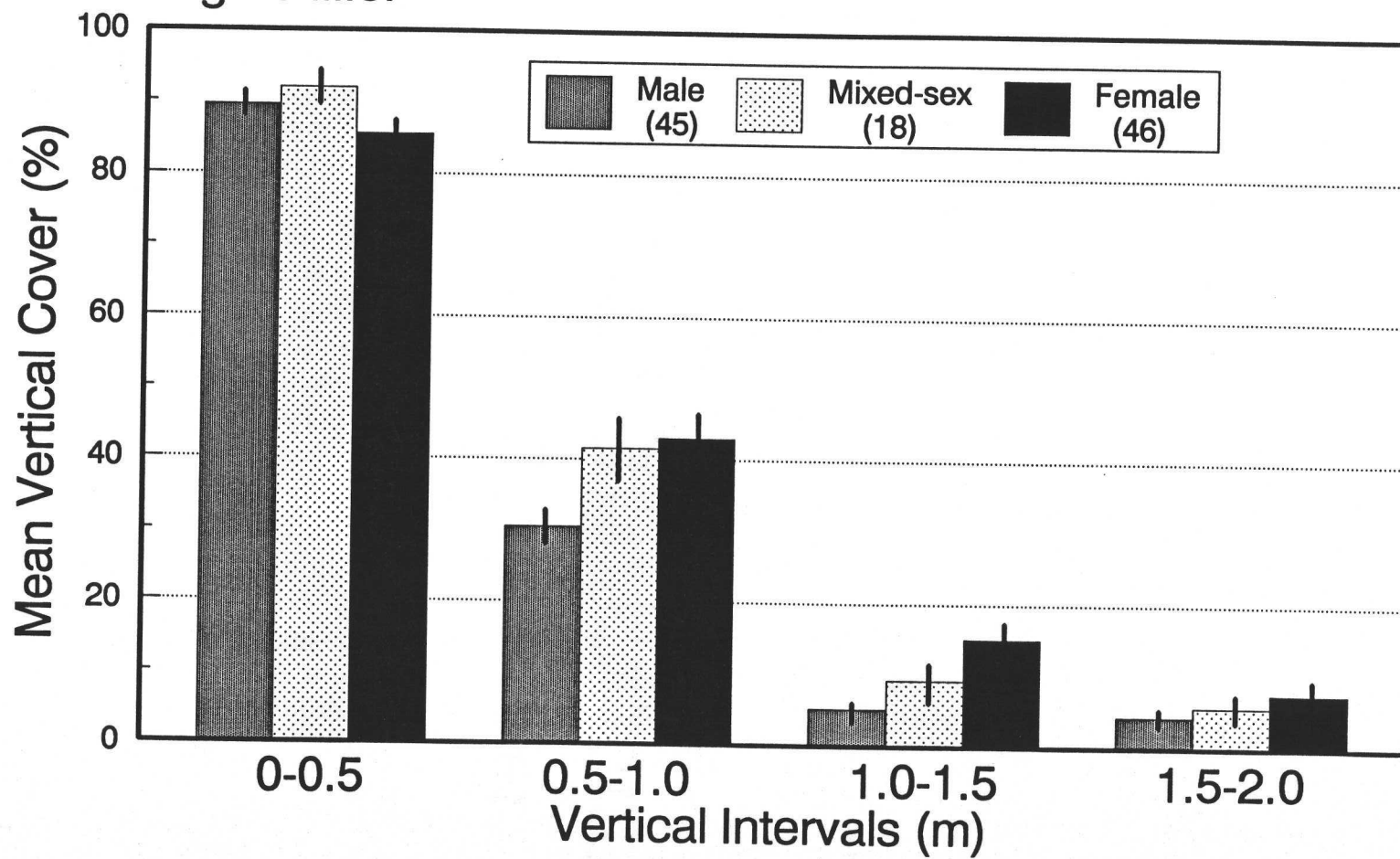


Figure III.8.



Discussion

Intersexual differences in spatial distribution have been documented for mule deer at HMNAR (Main, 1994; Chapter 4), and the results of this study suggest that the distribution of female groups was strongly influenced by the availability of resources that provided security for fawns from their major predator, coyotes. Coyote predation was not quantified in this study, but was found to be the major cause of mortality among mule deer fawns during a 12-year study on nearby Steen's Mountain (Trainer et al., 1981). Cougars (Felis concolor) were presumed to exert less predation pressure than coyotes because no evidence of cougar presence was observed in the study area during three field seasons.

Reactions to coyotes differed between the sexes. Adult female mule deer observed with fawns reacted very aggressively toward coyotes and were often observed chasing them, a defensive behavior reported elsewhere (Bowyer, 1987; Griffith, 1988; Hines, 1975; Riley and Dood, 1984). While females demonstrated strong reactions to coyotes, males generally displayed little interest and rarely appeared alarmed when in the presence of coyotes. There was no evidence that male distribution or behavioral patterns were influenced by coyotes or other predators.

Females increased fawn security from coyotes in several ways, one of which was by using slopes $\geq 10^\circ$, which were avoided by coyotes (Fig. III.2.). This strategy was used most during the JJ-JA parturition-postpartum period when fawns were dependent on crypsis or maternal defense (Fig. III.3.). Coyotes were observed almost exclusively on level terrain, a behavioral or hunting pattern that has also been described by Riley and Dood (1984). As the summer progressed female groups gradually decreased their

use of slopes $\geq 10^\circ$, a response that paralleled fawn growth and the development of motor skills. Male groups used all slope types, but used level terrain significantly more than female groups (Fig. III.2.) and demonstrated no seasonal patterns.

Female groups also used feeding sites that supported significantly greater horizontal (Table III.5.) and vertical (Fig. III.8.) shrub cover than typically used by male groups. Regardless of the role of slope gradient, it was clear that female sites in all cover-types typically supported denser and higher shrub cover than areas used by males. Seasonal patterns related to protective cover were evident among female but not male groups. Female groups increased their use of GRASS cover-types (Fig. III.1b.) and used feeding areas with significantly less horizontal shrub cover (Fig. III.7.) as fawns matured. Compared to shrub-dominated communities, GRASS cover-types provided poor hiding cover. Consequently, exploitation of this cover-type represented a trade-off in terms of exposure risk versus foraging opportunities. Female groups also increased their use of BIT cover-types during AO (Fig. III.1b.), which probably reflected an increased use of bitterbrush as a fall food resource (Carson and Peek, 1987; Kufeld et al., 1973; Leckenby et al., 1982; Wilkins, 1957).

Daily movement patterns also influenced fawn security. Among species that actively defend offspring, adults should minimize the amount of time spent distant from offspring. Resource distribution directly influences the distances traveled and time spent separated from bedded offspring, or the exposure risk (as related to travel distance) for offspring at heel. Female ungulates characteristically have smaller home ranges than mature males (Beier and McCullough, 1990; Clutton-Brock et al.,

1982; Eberhardt et al., 1984; Nelson and Mech, 1981; Robinette, 1966). Mule deer movement patterns were consistent with this at HMNAR; female groups concentrated their activities in smaller areas and were much more predictable in their locations than were male groups. The apparent consequence of localized female movements was the depletion of forb biomass at female feeding sites (Main, 1994; Chapter 4). The depletion of forb biomass may explain why female groups were much more likely to be observed in cover-types that supported stands of palatable browse (MESIC, BIT; Table III.2.), and at feeding sites with significantly higher species richness and cover for the most palatable browse species (Table III.4.). Although browse was not identified as the major diet item for either sex during June-September 1988 at HMNAR (Main, 1994; Chapter 4), the greatest proportion of browse found in female diets occurred during the peak fawning period when females typically restrict movements most (Beier and McCullough, 1990; Ozoga et al., 1982). Females also used N-E aspects significantly more than males at this time, a pattern that reflected female use of MESIC cover-types (Fig. III.1b.) and steep slopes (Fig. III.3.). These results suggested palatable browse enabled female groups to maintain localized foraging behaviors when forbs became scarce from over-utilization or environmental conditions, and was an important factor regulating the distribution of female groups at HMNAR. In contrast, male groups were observed primarily in MBS (71% of observations). MBS communities were dominated by mountain big sagebrush which is a poor summer forage (Kufeld et al., 1973; Roche, 1983; Sheehy, 1975) and was rarely observed being eaten by either sex.

Water availability also influenced movement and distribution patterns. Females were observed

significantly closer to water than males during July-September at HMNAR (Fig. III.6.). Similar results have been reported elsewhere for mule deer (Bowyer, 1984; Leckenby et al., 1982), desert bighorn (Ovis canadensis nelsoni; Bleich, 1993), Grevy's zebra (Equus grevyi; Becker and Ginsberg, 1990), and African elephants (Loxodonta africana; Corfield, 1973). Lactating mule deer require water daily and must return to bedded fawns (Elder, 1956; Leckenby et al., 1982). Consequently, water availability imposes energetic (Moen, 1973) as well as security constraints. In contrast, males can forage widely into areas far from water. Males at HMNAR were often observed >3 km from the nearest water source and often made diurnal movements between known water sources, a behavioral pattern not observed among female groups.

Elevational differences in male and female distribution at HMNAR may have been directly influenced by water availability because water was very scarce at high elevations. Similar elevational ranges used by males and females and observations of female/young groups at elevations above 2,300 m on nearby Steen's Mountain (personal observations), discouraged interpretations based on thermodynamic constraints (Parker, 1987; Parker and Robbins, 1985). Only males demonstrated trends in seasonal elevation; males used higher elevations as the season progressed (Fig. III.4.), which may have reflected preferences for forbs in earlier phenological stages. The majority of mixed-sex groups occurred at intermediate elevations (Table III.3. and Fig. III.5.) and were typically observed in canyon systems that supported MESIC cover-types and comparatively high herbaceous biomass (Main, 1994; Chapter 4). These results suggest that mixed-sex groups represented temporary aggregations of

separate male and female groups attracted to desired resources, including water.

Polygynous ungulate females tend to be philopatric and demonstrate strong site fidelity both seasonally and yearly (Clutton-Brock et al., 1982; Garrott et al., 1987; Nelson, 1993; but see Berger, 1986). These behavioral patterns may eliminate many of the risks associated with dispersal and raising offspring in unfamiliar or unpredictable environments (Shields, 1987). Consequently, areas that provide adequate security and resources favor the development and persistence of extended matrilineal groups. Coyotes may represent an important selective pressure influencing the distribution of persistent female groups at HMNAR. This hypothesis is supported by the results of long-term coyote predation studies at nearby Steen's Mountain (Trainer et al., 1981) and the abundance of coyotes at HMNAR. The results of this study suggested female groups at HMNAR used areas that reduced the risk of contact between fawns and coyotes and provided greater security for fawns relative to areas used by males, particularly during the first eight weeks postpartum. Areas used by females supported palatable browse and were close to water, two factors that enabled female groups to minimize travel. Furthermore, reduced forb biomass at female feeding sites suggested that females restricted feeding efforts to areas that provided greater security even at the expense of losing superior foraging opportunities, paralleling results obtained for other ungulates (Berger, 1991; Bergerud et al., 1984; Bleich, 1993; Jakimchuk et al., 1987; Miquelle et al., 1992). The tendency for females to use areas of greater predation risk as fawns matured, suggested that as fawns became less dependent on crypsis and maternal defense, females expanded their feeding efforts. Males, unconstrained by

offspring needs, should be more plastic in habitat requirements. Since selective pressures influencing male breeding success are related to body size and energy reserves, males optimize energy intake and feed in areas avoided by female groups despite increased risks from potential predators (Prins and Iason, 1989).

INTERSEXUAL COMPETITION AND PROXIMATE MECHANISMS
INFLUENCING SEXUAL SEGREGATION BY MALE MULE DEER
CHAPTER 4

Abstract

Sexual segregation was documented in a herd of mule deer (Odocoileus hemionus hemionus) during May-October at Hart Mountain National Antelope Refuge, Oregon. Forbs were the major diet component in both male and female diets and proximate causal factors for segregation by males were attributed to the effects of localized female feeding patterns, female site fidelity, and larger female feeding groups on forb biomass. Males ranged over larger areas than females, a strategy that provided a diet high in forbs and of higher or comparable quality to female diets. There was no evidence that agonistic behavior by adult females maintained segregation by mature males. The occurrence of mixed-sex groups in highly productive areas further suggested that sexual segregation was not due to antagonism or other social factors between adult males and females, but was a male response to the availability of preferred diet items.

Introduction

Selander (1966) outlined three ways in which a species can expand its ecological sphere or niche while simultaneously reducing intersexual competition for food. These include taking food items of different sizes, using different foraging techniques, or foraging in different areas. The latter describes sexual segregation, a behavioral pattern where conspecific sexes live separately during all or part of non-breeding periods. This behavior has been documented among various taxa and is prevalent among polygynous ungulates (see reviews in Bleich, 1993; Main and Coblentz, 1990; Miquelle et al., 1992).

Among ungulates, and in most polygynous species, males are considered the dispersing sex while females tend to be philopatric and show strong site fidelity (Albon et al., 1992; Clutton-Brock et al., 1982; Greenwood, 1980; McCullough, 1979; Nelson, 1993; but see Berger, 1986). After dispersing, mature male ungulates generally avoid re-associating with female groups except during breeding periods and may, therefore, be considered the segregating sex.

The reasons males remain segregated during nonbreeding periods has been a subject of debate (Main and Coblentz, 1990; Weckerly, 1993). Hypotheses proposed to explain sexual segregation among ungulates have been reviewed in detail by Main and Coblentz (1990) who argued that sexual segregation occurs due to different reproductive strategies; males should attempt to maximize weight gain to increase reproductive competitiveness while females should inhabit areas with resources suitable for raising offspring, even at the expense of reduced foraging opportunities. Specific tests of this and other hypotheses have recently supported Main and Coblentz

(1990) regarding the ultimate impetus for sexual segregation for desert bighorn sheep (Ovis canadensis nelsoni; Bleich, 1993:96), moose (Alces alces; Miquelle et al., 1992:45), and black-tailed deer (Odocoileus hemionus columbianus; Weckerly, 1993:491). However, there is still no consensus regarding the proximate mechanism that maintains segregation when females appear to inhabit better quality habitat (Beier and McCullough, 1990). Potential explanations proposed to explain this apparent incongruity include segregation as a result of 1) intersexual competition for forage (Clutton-Brock et al., 1987; Ilius and Gordon, 1987); 2) social factors related to assessment of potential male rivals and female breeding partners (Beier and McCullough, 1990; McCullough, 1979); and, 3) the potential ability of males to subsist on poorer quality forage due to allometric relationships related to size dimorphism (Beier, 1987; Beier and McCullough, 1990; Bowyer, 1984; McCullough, 1979). Although males may benefit from knowledge of the distribution of potential mates and from developing pre-rut dominance relationships with other males, this has not been demonstrated and has been rejected as the primary impetus for sexual segregation in white-tailed deer by Main (1994; Chapter 5). Additionally, although the third explanation may explain how males are able to survive in poorer quality habitat, it fails to explain why they would choose to do so, and has been rejected as an explanation for segregation in black-tailed deer (Weckerly, 1993).

The objectives of this study were to 1) document patterns of sexual segregation in an eastern Oregon herd of Rocky mountain mule deer (O. hemionus hemionus) during May-October; 2) to determine whether evidence existed to support the hypothesis that sexual segregation provided males with superior foraging opportunities when females

predominated in mesic habitats; and, 3) to determine whether segregation was consistent with explanations attributable either to direct (interference) or indirect (scramble) competition for preferred forage.

Study Area

This study was conducted on 14,000 ha of the 111,336 ha Hart Mountain National Antelope Refuge (HMNAR) in southeastern Oregon. Study area elevation ranged from approximately 1,500-2,100 m above sea level. HMNAR is contained within the northern boundary of the Great Basin Desert (42°32'N, 119°40'W) and has a semi-arid climate with annual precipitation occurring primarily as snow (50 year annual mean = 29 cm; USFWS, unpublished refuge records). Vegetation at HMNAR has been classified as shrub-steppe (Franklin and Dyrness, 1973) and is dominated by mountain big sagebrush (Artemisia tridentata tridentata) with stands of quaking aspen (Populus tremuloides), choke and bitter cherry (Prunus spp.), and snowbrush (Ceanothus velutinus) in mesic areas and Western juniper (Juniperus occidentalis) and curlleaf mountain mahogany (Cercocarpus ledifolius) on xeric south slopes and ridge tops.

Methods

Preliminary field work was conducted 1 June-25 September 1988; the results of which were used to develop the final research design for two subsequent field seasons (15 June-15 October 1989 and 1 May-15 September 1990). Two observation periods were conducted while deer were on winter range during 1-15 January 1989 and 1-15 March 1990. While on winter range, deer herded in large mixed-sex groups and displayed minimal activity. With the exception of diet information, all methods described and data analyzed in this paper were restricted to information collected during May-October during the 1989 and 1990 field seasons.

Survey routes encompassing established transects and vantage points were walked or driven with the help of two field assistants at dawn and dusk approximately five days each week. Three routes each were established in typically male and female areas and schedules were arranged to provide equal effort among areas occupied by each sex class.

Deer groups (≥ 1 deer) represent the statistical sample units unless noted otherwise. Deer group-types were defined as male, female, or mixed-sex based on the presence of adult individuals. Deer were considered within the same group based upon proximity, direction of movement, and behavioral responses among group members. Yearling groups with no adults were rare during the study period and were not included in statistical analyses. Fawns were excluded from statistical analyses and calculations of average group sizes because the influence fawns have on available forage (i.e., competitive effect) is minimal relative to that of adults and yearlings and to

include fawns in calculations would misrepresent the effects of group size.

Deer locations were plotted on 7.5 minute USGS topographic maps while in the field and categorized into 64 ha activity cells. The use of activity cell data as a basis for the detection of differences in spatial distribution is dependent upon the size of the cell; the 64 ha cell size analyzed in this study was considered a conservative measure. Spatial segregation (overlap) was calculated with Schoener's (1968, 1970) index using total individuals (excluding fawns) for comparison with previous studies (Clutton-Brock et al., 1987; McCullough et al., 1989; Miquelle et al., 1992). Schoener's index was calculated as $C_{ih} = 1 - \frac{1}{2} \sum |P_{ij} - P_{hj}|$, where C_{ih} is the overlap of sex "i" on sex "h" and P_{ij} and P_{hj} are the proportions of sex "i" or "h" in grid cell "j", respectively. Values for C range from 0 (no overlap) to 1 (complete overlap). Significance tests are not available for overlap indices. In order to make direct statistical tests of spatial distribution, log-linear models and G-tests were used to test for differences in observed versus expected frequency distributions after activity cells were defined by group-type (Miquelle et al., 1992; Sokal and Rohlf, 1981). Deer groups, rather than individuals, were used in log-linear and G-test analyses to avoid violating assumptions of independence.

Activity cells were also categorized by number of repeat observations by group-type ($n = 1-3$, $4-9$, and ≥ 10 observations/cell/year) in order to provide a measure of the level of activity in cells and to examine the influence of this on segregation. Log-linear models and G-tests were used to identify deviations from expected frequency distributions. Pearson product-moment correlations were calculated for activity cells with ≥ 4

observations per cell. Only cells with ≥ 4 observations were used in correlations to avoid the influence of cells typically avoided by deer, or by cells that were difficult to survey.

Home range data was obtained during June-September 1990 for three adult females, and July-September 1990 for one 2.5 year old male, all of which were captured using xylazine-ketaset mixtures (Jessup et al., 1983) and outfitted with radio-collars (Telemetry Systems, Inc.). Location information was collected by visually locating each animal approximately two times each week. Home range was calculated by the minimum convex polygon (MCP) method with the McPaal^R computer software program (Stuwe and Blohowiak, 1985).

All observed agonistic interactions were recorded during behavioral observations in an all-occurrences log (Altmann, 1974). Aggressive acts were recorded in an attempt to determine whether direct competition was occurring inter- and intrasexually for space or resources. Descriptions of aggressive acts followed those provided by Hirth (1977). Sparring between males was not treated as an act of aggression because the objectives of this activity are not intended to harm or supplant another individual from a resource. No instances of male combat for female breeding partners were recorded during May-October. Statistical comparisons of the proportion of total acts directed by males toward females and vice versa were conducted with a G-test (Sokal and Rohlf, 1981).

Microhistological techniques (Sparks and Malechek, 1968) were used to analyze fecal samples collected from adults of known sex during the 1988 field season. Multiple pellet groups were collected and composited (Leopold and Krausman, 1987) by group-type and month ($n \geq 10$ samples/sex/month) during June-September. Percent

composition of diets was estimated by forage class (forb, browse, grass) and based on 100 views per diet with an additional 50 views per correction factor. Correction factors were calculated to compensate for differential digestibilities of different forage items (Vavra and Holechek, 1980). All analyses were conducted by the Washington State University Wildlife Habitat Laboratory. Statistical analyses of diets identified three deer group-types: females, males occurring in areas where females were scarce or absent, and males occurring in areas where females were common. Group-type and diet class were analyzed simultaneously with ANOVA. Significant differences among diet classes were compared using 95% Scheffe multiple-range tests.

Diet quality was measured directly for adult males and females by measuring diaminopimelic acid (DAPA) in composite fecal samples. DAPA, an indigestible amino acid residue from rumen microflora, increases as bacterial production increases and is positively correlated with diet quality (Kie and Burton, 1984; Leslie et al., 1989; Nelson et al., 1982), but does not suffer from confounding influences of secondary plant compounds as may fecal nitrogen (Hobbs, 1987; Robbins et al., 1987). Fecal samples were collected in the same manner as for diet analyses, except that male samples were not differentiated by area of collection. DAPA analyses were conducted by the Washington State University Wildlife Habitat Lab. Group-types and time periods were analyzed simultaneously with ANOVA and 95% LSD multiple range tests.

Herbaceous biomass was quantified separately for forbs and grasses (including grass-like, e.g., Carex spp.) during 1989 and 1990 at male, female, and mixed-sex feeding sites with a clip and estimate (double sampling) procedure (Hilmon, 1959). Plants clearly avoided by deer,

e.g., basin wildrye (Elymus cinereus), were excluded from biomass estimates. Dead vegetation was excluded from visual estimates and removed from clipped samples. Clipped samples were sorted, air dried for storage, dried for 48 hours at 50° C under controlled conditions, and weighed to the nearest 0.01 g with an electronic balance. Linear regression models were used to adjust unclipped estimates to dry weight, using clipped dry weights as the independent and field estimates as the dependent variables for each forage class, during each year (Forbs: 1989 $R^2 = 0.784$, $n = 271$; 1990 $R^2 = 0.746$, $n = 212$; Grasses: 1989 $R^2 = 0.642$, $n = 253$; 1990 $R^2 = 0.671$, $n = 344$). New sites were identified daily based upon observations of feeding groups. Approximately equal numbers of male and female sites were sampled, but fewer mixed-sex sites were obtained due to the infrequent nature of this group-type. Feeding sites were sampled in a stratified random manner (Pieper, 1978) with three 30 m transects, each with 10 rectangular plots (0.10 m²) positioned at 3 m intervals, within the general feeding area. Mean plot biomass/site was estimated as the mean of the three transect averages and represented the statistical sample unit. Grass and forb biomass was analyzed separately between years and simultaneously among time periods (6/15-7/15, 7/16-8/15, 8/16-9/15) and group-types with ANOVA. Differences among means were tested with 95% Scheffe multiple range tests. Plots of the residual versus the predicted values revealed an increase in the variances of the biomass data as the season progressed; a log transformation removed this effect and normalized the distribution. For graphical presentation, backtransformed means were reported with 95% confidence intervals rather than standard errors for reasons discussed by Sokal and Rohlf (1981:418).

Species richness, in vitro dry matter digestibility (IVDMD), and crude protein (CP) content were determined for living (green) forbs and grasses at feeding sites as a measure of relative site quality. Species richness was determined separately for grasses and forbs using total species counts (Peet, 1974), with mean species/transect/site the statistical unit used in analyses. Mean site values were log transformed and analyzed with ANOVA as for the biomass data. IVDMD and CP were analyzed separately for forbs and grasses using composite samples created by grinding clipped biomass samples collected during 1989. Composite samples, rather than individual species, were used because mule deer commonly include large numbers of species in their diets (Kufeld et al., 1973), actual diets were unknown, and a relative measure of site herbaceous quality was desired. IVDMD analyses followed a two-stage, microbial-gastric procedure (Tilley and Terry, 1963) and were conducted with rumen inocula from freshly killed black-tailed deer. CP was determined with kjeldahl procedures using an automated Buchi nitrogen determination system (Buchi 343 distillation unit). Site means based on multiple samples ($n \geq 2$ composite samples) were the statistical unit for IVDMD and CP. ANOVA and 95% Scheffe multiple range tests were used to test for differences among group-types and time periods.

The Statgraphics^R (STSC) statistical computer software package was used to conduct analyses using log-linear models, Pearson product-moment correlations, linear regressions, and ANOVA, all of which are described in Sokal and Rohlf (1981). Data transformations were used as necessary based upon examination of residual probability plots and plots of residuals versus predicted values.

Results

Mule deer at HMNAR segregated by sex during May-October; 93% of all deer groups observed during May-September were single-sex while mixed-sex groups increased to 12% during October. Schoener's (1968) index of overlap was calculated from observations of 4,537 individuals and indicated sexual segregation was pronounced (Table IV.1.). Statistical tests of distribution were based on locations of 1,487 female, 431 male, and 135 mixed-sex groups; no differences were detected in activity areas used between 1989 and 1990 ($\chi^2 = 0.052$, $P = 0.82$), so years were pooled. Spatial distribution differed significantly among group-types ($\chi^2 = 93.27$, $P < 0.0001$), and differed between male and female groups ($G = 66.79$, $P < 0.001$), but not between mixed-sex and either male ($G = 3.628$, $P > 0.05$) or female groups ($G = 0.433$, $P > 0.05$). Mixed-sex groups occurred more often in cells with observations of female groups (90%) than male groups (72%), but this difference was not statistically significant ($G = 1.559$, $P > 0.05$).

Table IV.1. Indices of spatial overlap (C ; Schoener, 1968) between males and females from this and other studies. Complete segregation, $C = 0$, complete overlap, $C = 1$.

Species	Period	Quadrat Size (m ²)	C
Mule deer ¹	May-Oct.	640,000	0.311
White-tailed deer ²	Apr.-Oct.	10,120	0.574
Red deer ³	May-Aug.	10,000	0.364
Moose ⁴	July-Aug.	2,560,000	0.572

¹This study; $C = \bar{X}$ of 1989 and 1990

²McCullough et al. (1987)

³Clutton-Brock et al. (1987); $C = \bar{X}$ of years & cover-types

⁴Miquelle et al. (1992)

Total observations by cell differed significantly among group-types ($\chi^2 = 439.0$, $P < 0.0001$). Mixed-sex groups were typically observed ≤ 3 times in any given cell (Fig. IV.1.; $G = 10.82$, $P < 0.001$) and were never observed ≥ 10 times in any cell. Male groups were equally likely to be observed in cells with 1-3 or 4-9 repeat observations, but were significantly less likely to be observed in cells with ≥ 10 repeat observations ($G = 92.86$, $P < 0.001$). Activity was highest in cells used by female groups, which were significantly more likely to be observed ≥ 10 times in any given activity cell ($G = 329.0$, $P < 0.001$). Cells with ≥ 10 observations constituted a significantly larger proportion of the total area used by females compared to males (females = 16%, males = 2.1%; $G = 37.85$, $P < 0.001$), and females were the only group type with over 25 observations in any given cell (4.3% of total cells).

In addition to having significantly more repeat observations in cells, the average number of deer per group (excluding fawns) was significantly larger for females than males (Table IV.2.; $t = 3.49$, $P < 0.001$). Consequently, the average number of individuals observed in cells (an approximation of density) was more than twice as large for females as for males in cells with > 3 group observations. The average number of deer in mixed-sex groups was significantly larger than that of female ($t = 7.70$, $P < 0.001$) or male groups ($t = 11.42$, $P < 0.001$), the effect of which would be to increase activity in cells used by both sexes, particularly in cells used by females due to the greater occurrence of mixed-sex groups in these areas.

The tendency for female groups to be observed repeatedly within cells suggested localized movement patterns and seasonal site fidelity. Quantitative data consistent with localized movement patterns was provided

by three radio-collared females that had a mean home range of 1.09 km^2 ($\text{SD} = 0.8$) during June-September 1990 (locations/female: $\bar{x} = 47$, $\text{SD} = 8.9$). Additionally, evidence that female groups displayed annual site fidelity was provided by observations of female groups in the same areas each field season and from observations by refuge biologists of collared females returning to their 1990 home range in successive years (W. Pyle, pers. comm.). Based on observed movement patterns of male groups, males ranged over much larger areas than females, and the home range of a radio-collared 2.5-year male during July-September 1990 was approximately twice that calculated for females (2.14 km^2 , $n = 28$ locations).

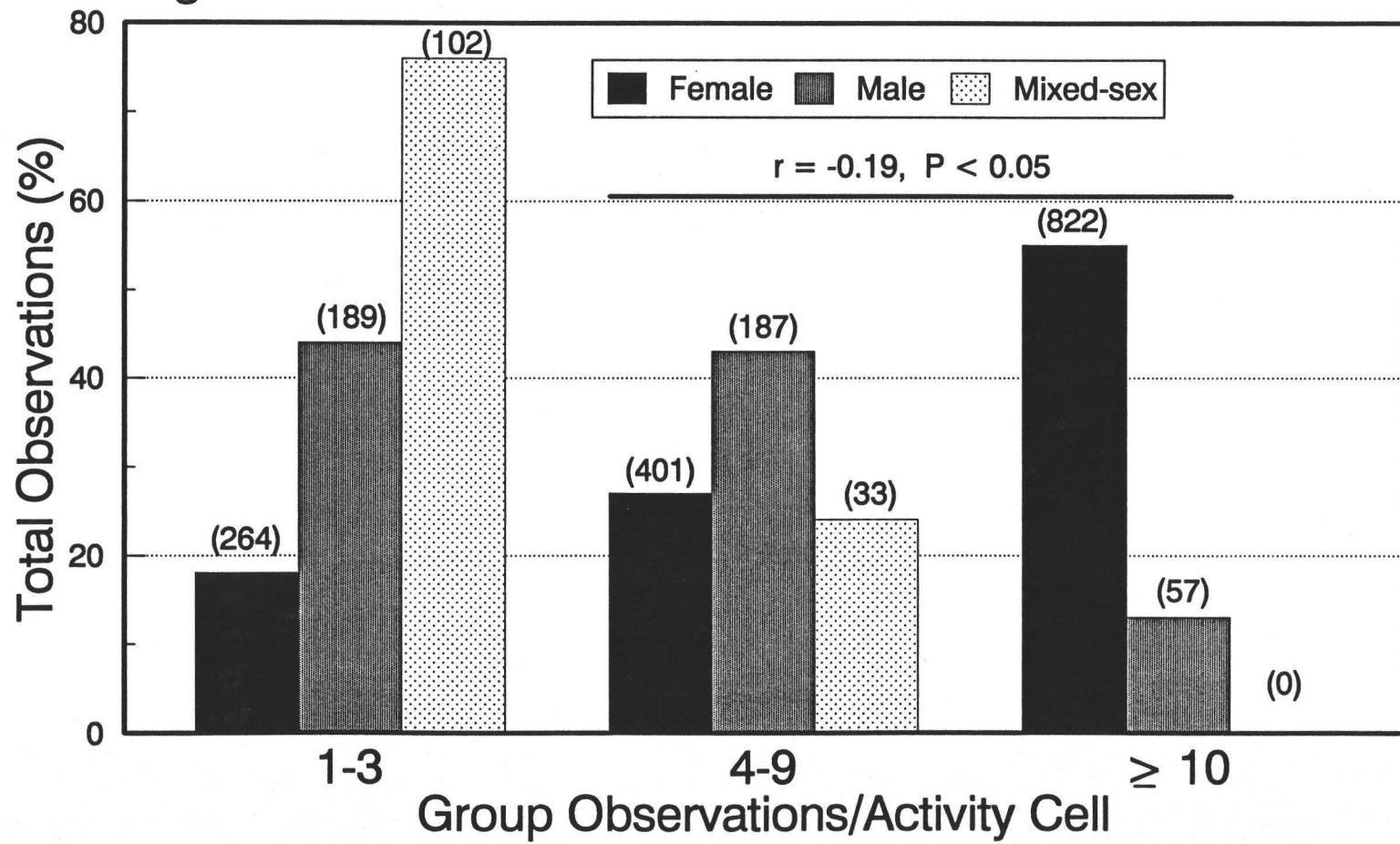
The data suggested that cells experiencing high use by one sex were avoided by the other. A significant negative correlation existed between male and female observations in activity cells with ≥ 4 group observations by either sex ($r = -0.19$, $\text{d.f.} = 128$, $P < 0.05$). This effect was even more pronounced in cells with very high levels of use by females; of the 40 cells with ≥ 10 female group observations, only six cells had more than three male observations and 22 had zero ($r = -0.32$, $\text{d.f.} = 40$, $P < 0.05$).

Table IV.2. Mean group size for male, female, and mixed-sex deer groups during May-October 1989 and 1990. Statistical comparisons determined by t-tests; nonaligned asterisks represent statistical differences among group-types at $P < 0.05$.

Group-type	n	Group Size		t-test Comparisons
		Mean	SE	
Male	494	2.67	0.08	*
Female	1,688	3.12	0.07	*
Mixed-sex	164	4.66	0.21	*

Figure IV.1. Intensity of cell use by male, female, and mixed-sex groups, measured as the percentage of total groups observed in each of three repeated observations/activity cell categories. Total deer groups in parentheses.

Figure IV.1.



Aggression between adult males and females was rare. Behavioral observations of 158 mixed-sex groups during 1989 and 1990 produced only seven instances of agonistic interaction between adult males and adult females, and adult males dominated in six of these. Although aggression between adult males and females was rare, the proportion of total aggressive acts directed by males toward females was significantly greater than the opposite ($G = 8.29$, $P < 0.01$). While adult males dominated adult females, adult females dominated yearling males, being the aggressor in 22 of 24 (92%) observed agonistic interactions.

Forbs, at over 80%, were the most important dietary component for both sexes (Fig. IV.2.). Forb, browse, and grass forage classes constituted significantly different proportions of deer diets during June-September ($F = 112.8$, $P < 0.0001$). Forbs predominated in diets of both sexes, and browse was significantly greater than grasses for all group types ($P < 0.05$). Diets were statistically similar between females, males, and males from areas where females were common ($F = 0.029$, $P > 0.05$), although forbs were consumed less and browse more by males from the latter category. Although male and female diets were similar in composition, they differed in quality. Diet quality, as measured by DAPA, differed between males and females with males having diets of significantly higher quality during June and July ($P < 0.05$; Fig. IV.3.). Diet quality decreased significantly over time for both sexes, and diets were similar during August and September (Fig. IV.3.).

Herbaceous biomass at feeding sites was significantly different between years, so years were examined separately. Although it was impossible to determine the reasons for the differences in biomass between years, it

is likely these differences were due to reduced precipitation during 1990 and continued drought since 1988. Precipitation at HMNAR during May-September 1988, 1989, and 1990, was 73, 70, and 59 percent of the 50 year average, respectively (50 yr. $\bar{X}$ = 11.77 cm; HMNAR, unpubl. refuge records). Herbaceous biomass followed similar annual patterns, with significant differences among group-types and time-periods for both grasses and forbs during 1989 and 1990. Female feeding sites had significantly lower average forb biomass than either male or mixed-sex feeding sites during both years ($P < 0.05$; Fig. IV.4.). Although male and mixed-sex feeding sites were statistically similar, mixed-sex feeding sites included some of the most productive areas and had the highest average forb biomass during both years. Average grass biomass was also significantly lower at female sites than at either male or mixed-sex sites during 1989, but only mixed-sex and female sites were significantly different during 1990 ($P < 0.05$; Fig. IV.5.).

Forb and grass species richness differed significantly between years, so 1989 and 1990 data were analyzed separately. Forb species richness followed consistent annual patterns during 1989 and 1990; species richness declined significantly over time and differed among group-types (Fig. IV.6.). During both years, male and mixed-sex feeding sites were similar and had significantly more forb species than found at female sites ($P < 0.05$). Grass species richness also followed consistent annual patterns. Although grass species richness did not differ among time periods, male feeding sites had significantly greater ($P < 0.05$) species richness than female sites and mixed-sex sites were intermediate (Fig. IV.7.). Relative site quality was similar among group-types. Neither grasses nor forbs

differed for IVDMD (Forbs: $F = 0.08$, $P = 0.92$; Grasses: $F = 2.93$, $P = 0.07$) or CP (Forbs: $F = 1.01$, $P = 0.37$; Grasses: $F = 1.60$, $P = 0.21$) among group-types. However, significant declines occurred in both IVDMD (Forbs: $F = 8.24$, $P = 0.001$; Grasses: $F = 11.76$, $P = 0.0001$) and CP (Forbs: $F = 27.56$, $P < 0.0001$; Grasses: $F = 21.52$, $P < 0.0001$) over time.

Figure IV.2. Percent composition (with SE) of major forage classes in diets of adult males (from areas where females were rare or absent), females, and males from areas where female activity was common (designated as mixed-sex) during June-September 1988.

Figure IV.3. Concentrations (with SE) of diaminopimelic acid (DAPA) in composited fecal samples from adult male and female mule deer during June-September 1988.

Figure IV.4. Mean forb biomass (with 95% CI) by dry weight at female, male, and mixed-sex feeding sites during 15 June-15 September 1989 and 1990. Total number of feeding sites in parentheses.

Figure IV.5. Mean grass biomass (with 95% CI) by dry weight at female, male, and mixed-sex feeding sites during 15 June-15 September, 1989 and 1990. Total number of feeding sites in parentheses.

Figure IV.6. Mean forb species richness (with SE) per 30 m transect at male, female and mixed-sex feeding sites during June-September 1989 and 1990. Species richness determined by direct counts.

Figure IV.7. Mean grass species richness (with SE) per 30 m transect at male, female and mixed-sex feeding sites during June-September 1989 and 1990. Species richness determined by direct counts.

Figure IV.2.

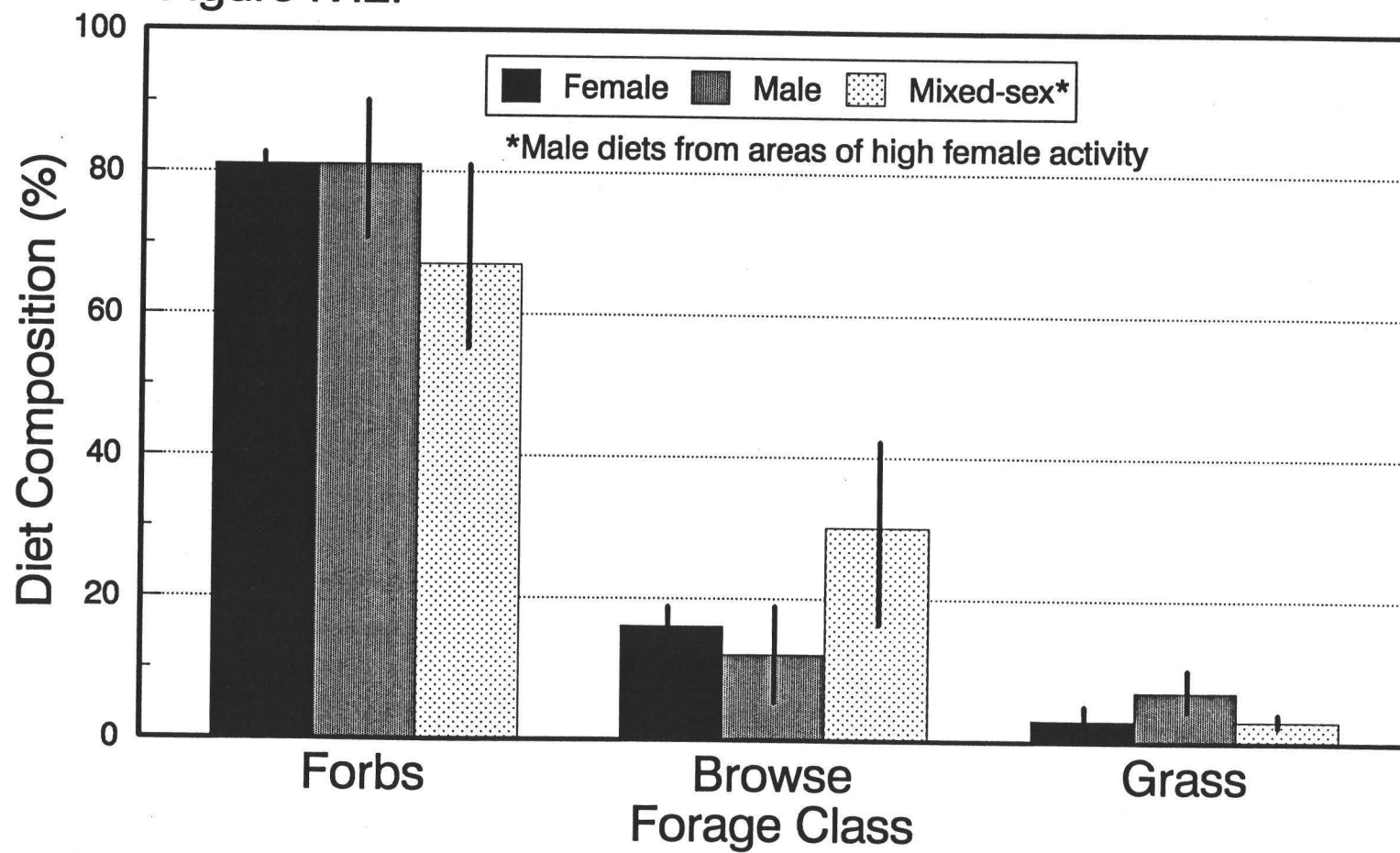


Figure IV.3.

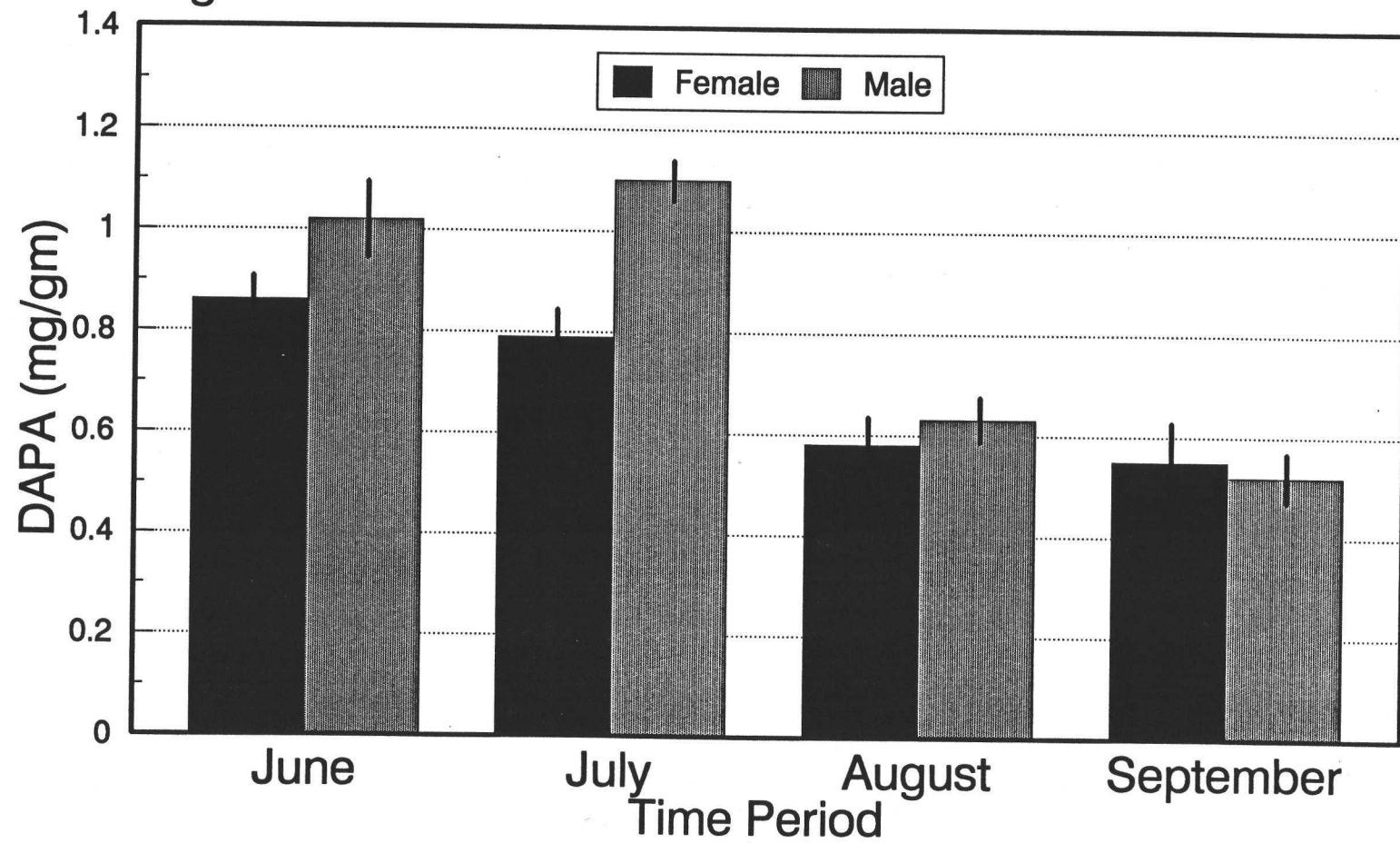


Figure IV.4.

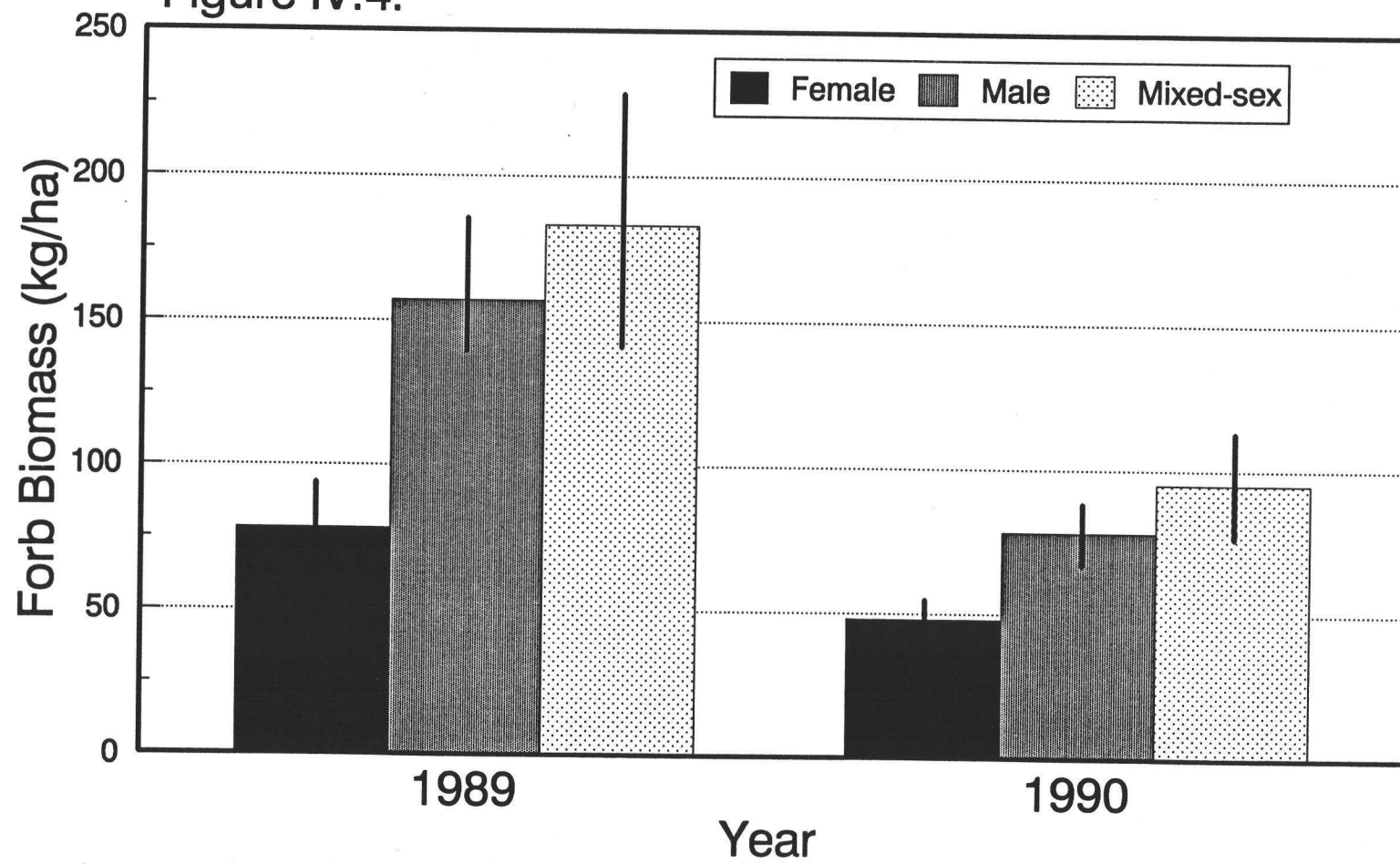


Figure IV.5.

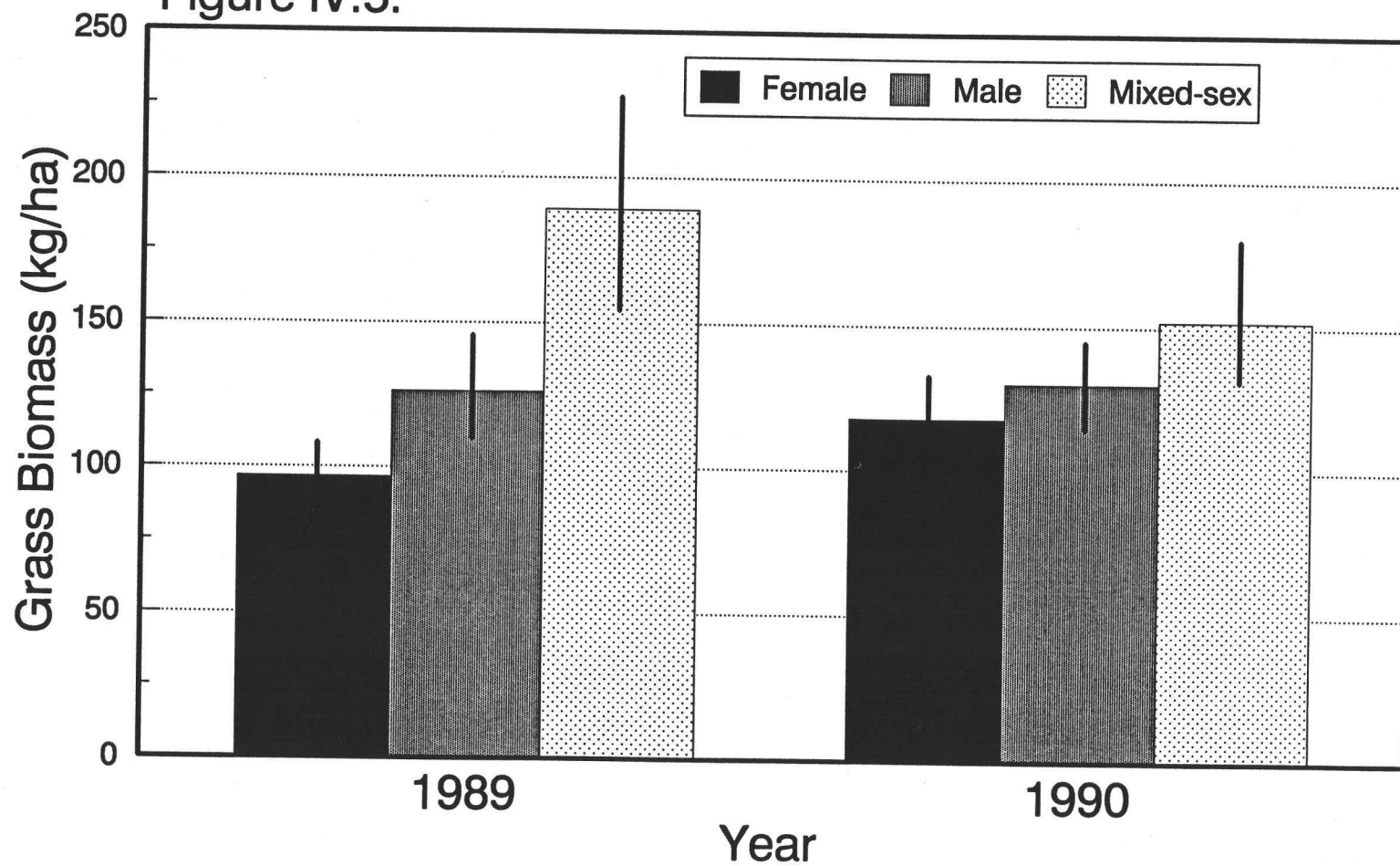


Figure IV.6.

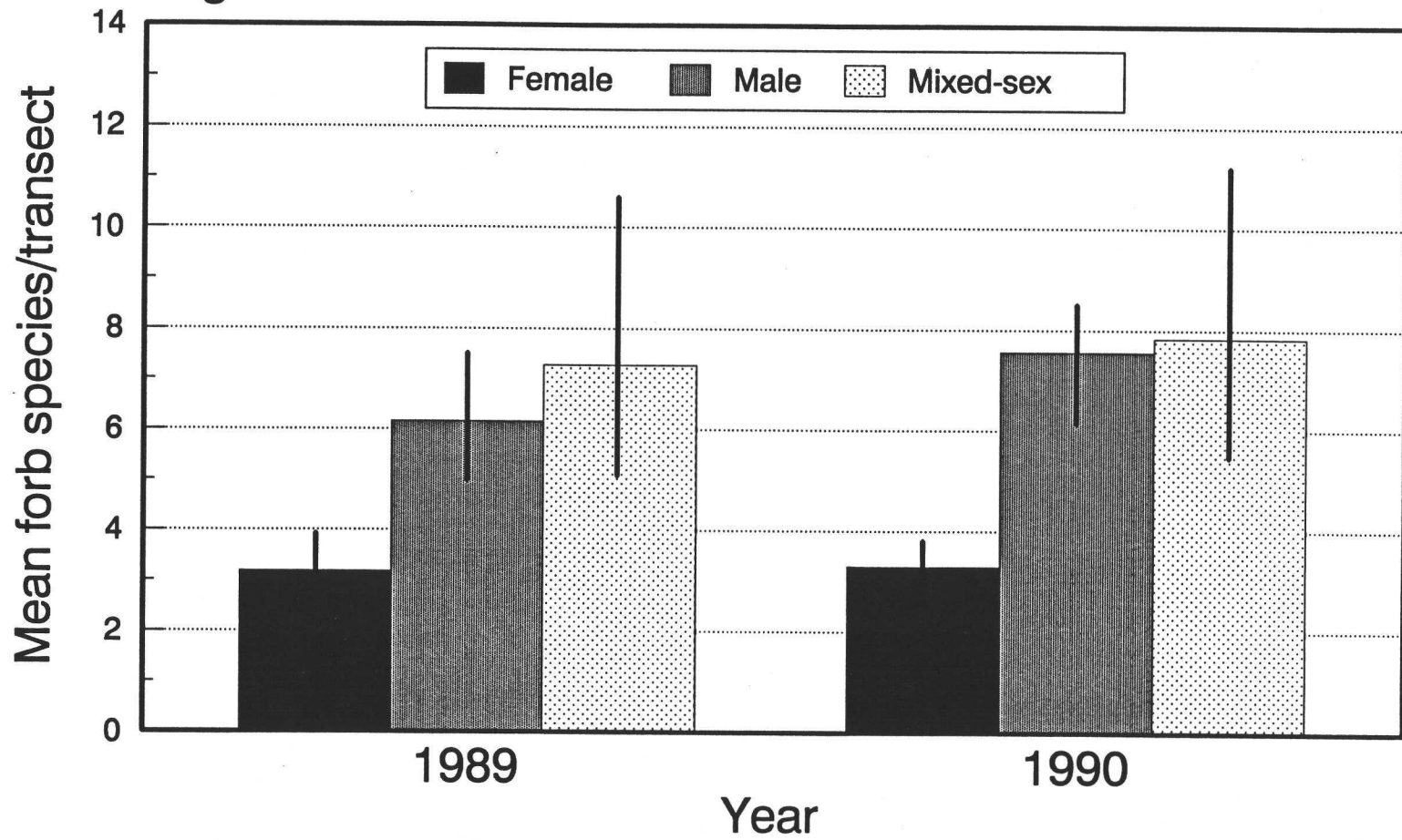
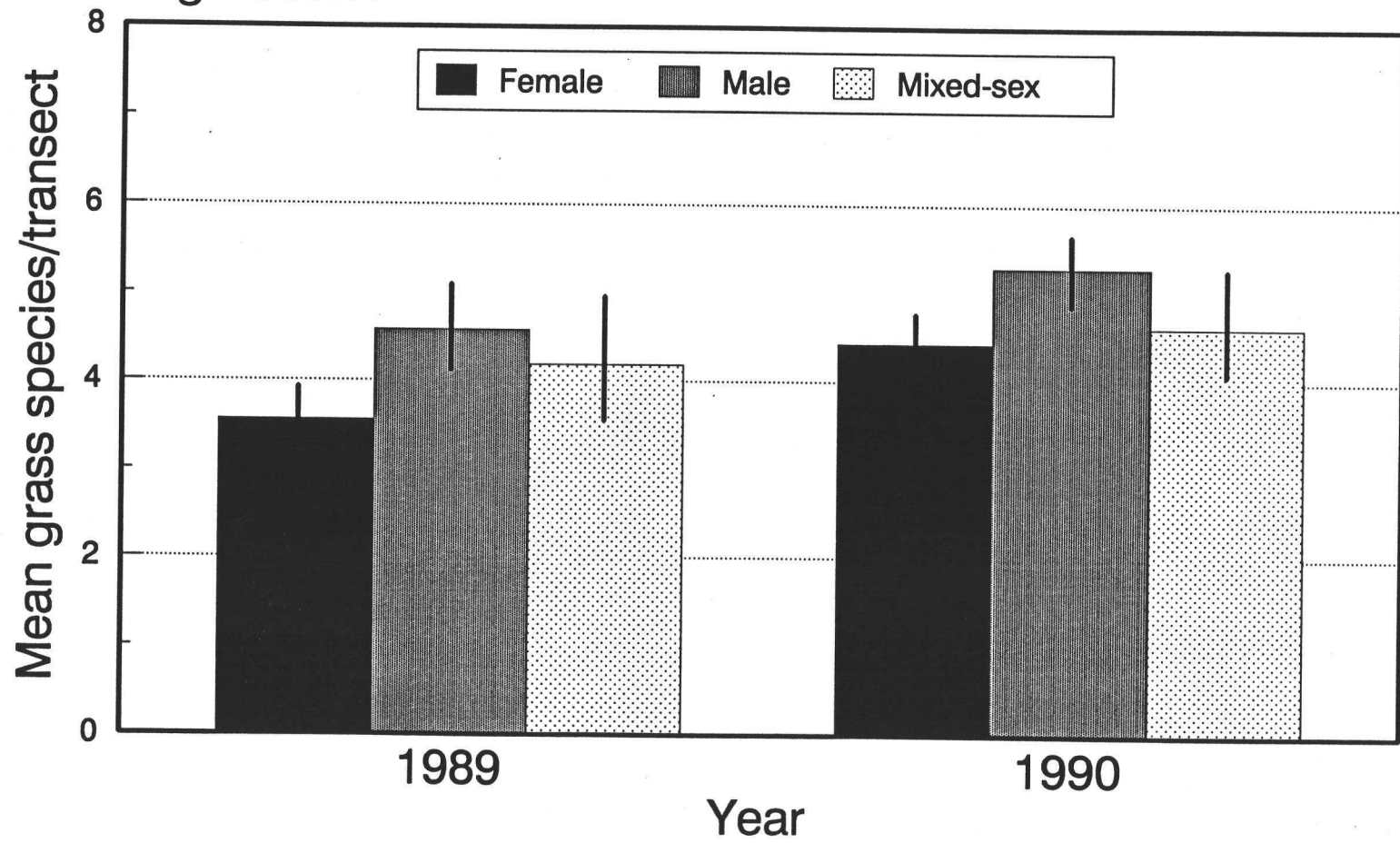


Figure IV.7.



Discussion

Sexual segregation was pronounced among mule deer at HMNAR in both social and spatial contexts during May-October. The negative correlation observed between male and female groups in activity-cells with ≥ 4 , and particularly among those cells with ≥ 10 female group observations, suggested that one or both sexes avoided areas used by the opposite sex and that avoidance was related to the level of activity of the opposing sex.

Several studies of sexual segregation in ungulates have reported that females occupy better habitat than males (e.g., Beier, 1987; McCullough, 1979; Staines et al., 1982). However, the criteria used to evaluate habitat quality has often been questionable (see Main and Coblentz, 1990 for review). At HMNAR, female mule deer were predominant in areas that were more mesic, supported greater cover of palatable browse, provided greater security from coyotes, and were closer to water than areas used by males (Main, 1994; Chapter 3). From an observer perspective, these areas might appear to be better habitat than the xeric sagebrush flats typically used by male groups and the advantages of avoiding these areas would not be immediately obvious. However, when selective pressures, reproductive strategies, and preferred diet items were considered, several lines of evidence suggested that males avoided areas where female activity was high due to the competitive effects of localized female feeding pressure on preferred diet items.

Male mule deer, free from the constraints imposed by fawns, should be the more plastic of the sexes in terms of habitat requirements during periods when offspring are dependent upon parental care. In the absence of females, it seems likely that males would have utilized those areas

avoided where female activity was high. Observations supporting this argument included the occurrence of adult and subadult males in mixed-sex groups, the occurrence of activity cells used by both sexes, and males observed in vegetation cover-types both similar and different to those used by females (Main, 1994; Chapter 3).

There was no evidence that males avoided female areas because of agonistic female behavior. Male mule deer are considerably larger than adult females and were dominant in all but one agonistic interaction observed during 1989 and 1990. Similar dominance relationships have been reported for Odocoileus elsewhere (Hirth, 1977; McCullough, 1979; Ozoga, 1972). Typically, adult males and females ignored each other when in mixed-sex groups during nonbreeding periods, as reported for moose (Miquelle et al., 1992) and red deer (Cervus elaphus; Clutton-Brock et al., 1987). Adult females were dominant in agonistic interactions with yearling males and, while aggression by adult females may be an important factor in the initial dispersal of subadult males from female groups (Geist, 1981), there was no evidence that segregation of mature males was maintained by this mechanism.

A more likely explanation for male segregation was based on forage availability, specifically forbs, the predominant component in the diets of both sexes (Fig. IV.2.). Differences in forb biomass at male and female feeding sites appeared to be the consequence of different movement and feeding patterns exhibited by males and females. Males were highly mobile, often observed making diurnal movements >2 km, and were unpredictable as to location on any given day. Conversely, female groups rarely traveled far from areas where first observed, were very predictable in their locations, and were observed in the same activity cells much more frequently than male

groups (Fig. IV.1.). Radiotelemetry data from this study, while limited in scope, was consistent with these observations and consistent with other cervid studies that have determined females use smaller home ranges than males during spring-summer (Beier and McCullough, 1990; Clutton-Brock et al., 1982, 1986; Dasmann and Taber, 1956; Eberhardt et al., 1984; Mackie, 1970; Robinette, 1966). While restricted female movement has been attributed to the constraining influence of fawn requirements (Hines, 1975), observations of females that lost fawns and remained with their matrilineal units indicated that social bonds also influenced female movement patterns.

The apparent consequence of females concentrating feeding efforts over smaller areas and feeding in larger groups (Table IV.2.) was the reduction of forb biomass (Fig. IV.4.) and forb species richness (Fig. IV.6.), patterns that consistently occurred during both 1989 and 1990. Grass was a very minor diet component for both sexes, a finding consistent with other diet studies (Anderson et al., 1965; Uresk and Uresk, 1982). It was not surprising, therefore, that grass biomass was similar among male and female sites (Fig. IV.5.), although there was lower species richness at female sites (Fig. IV.7.). Despite reduced forb biomass in female areas, forbs were the most important diet component for both males and females (Fig. IV.2.), but male diets collected from areas where females were common had a lower forb and a higher browse component than did the diets of males from areas where females were scarce. Although these differences were not statistically significant, the possibility exists that these results represented a diet shift by males due to the influence of female grazing pressure in these areas.

The lower forb biomass observed at female feeding sites was not likely an artifact of site quality because 55% of female and 61% of mixed-sex feeding sites were located in mesic snowpocket or riparian communities with north and east facing aspects (Main, 1994; Chapter 3). Mesic communities, with greater soil moisture, should support greater forb biomass than the more xeric sagebrush flats where the majority of male feeding sites (61%) were located. Additionally, mesic sites might also be expected to produce forage of higher quality, as evidenced by the higher protein levels obtained in clover (*Trifolium* spp.) on irrigated soils (B. Davitt, Washington State University Habitat Lab, written communication). Although similar levels of forbs were found in male and female diets, the higher fecal DAPA (diet quality) observed for males during June and July (Fig. IV.3.) and the greater diversity of forbs found at male sites (Fig. IV.6.) suggested that male sites provided better foraging options than female sites, particularly since composite forb and grass samples had similar IVDMD and CP at male and female feeding sites. Similar DAPA levels between the sexes during August and September probably reflected the overall decline in forb quality due to phenological processes. It appeared then, that the ranging pattern employed by males enabled them to obtain a diet high in forbs and of as good, or better quality than diets obtained by females from sites receiving intense, localized foraging pressure.

Competitive dominance, defined as the suppression of one species (sex) by another, can result through the consumption of resources in limited supply, and will be manifested as a negative correlation in abundance (Keddy, 1989). Competitive exclusion, i.e., the premise that complete competitors cannot coexist (Hardin, 1960), may apply to intersexual as well as interspecific competitors

when those competitors have different life-history strategies. Clutton-Brock et al. (1987) suggested that heavy grazing pressure by female red deer (Cervus elaphus) may displace and competitively exclude males from greens (grasslands). Data collected during this study were consistent with this hypothesis, and suggested that female grazing pressure reduced forb biomass to the extent that areas where female activity was high were not attractive or suitable for males, i.e., females may have competitively excluded males from areas by reducing forb biomass.

Main and Coblentz (1990) argued that sexual segregation among ungulates should represent an attempt by males to maximize energy stores prior to the breeding period, while females should attempt to maximize security for offspring. The comparatively high herbaceous biomass found at male and especially at mixed-sex feeding sites suggests the distribution of males was in response to the availability of high quality forage, and not necessarily to the presence or absence of females per se, a result consistent with observations of mixed-sex assemblages feeding on agricultural crops or at winter feeding stations. While males may be excluded from areas where female grazing pressure depletes preferred forage, segregation by males may also occur strictly as a response to superior foraging opportunities that exist in areas avoided by females due to increased predation risks or other factors such as the availability of water (Berger, 1991; Bergerud et al., 1984; Bleich, 1993; Bowyer, 1984; Jakimchuk et al., 1987; Miquelle et al., 1992; Prins and Iason, 1989).

Sexual segregation, as observed among most polygynous ungulates, may have a common origin. The behavioral patterns reported in this and other studies suggest that

the proximate advantages of sexual segregation are directly related to the selective pressures influencing reproductive fitness. Because reproductive strategies and selective pressures influencing reproductive fitness differ between males and females (Clutton-Brock et al., 1988), it is not surprising that they cope with them in different ways. This study concentrated on the proximate advantages to males, and the results suggested that during the period when the accumulation of energy stores is most critical to males (Mautz, 1978), males maximized consumption of high quality forage. Because reproductive competitiveness requires males engage in an energetic race against time and against all other males, maximizing forage intake may require avoidance of areas where female activity depletes preferred forage. Consequently, conservative harvest strategies designed to expand or maintain high female numbers may eventually decrease available male habitat or relegate males to areas capable of supporting fewer mature animals in good condition.

SEXUAL SEGREGATION IN A POPULATION OF WHITE-TAILED DEER
IN A HOMOGENOUS ENVIRONMENT

CHAPTER 5

Abstract

Male and female white-tailed deer (Odocoileus virginianus), living at high densities in a relatively homogenous south Texas environment, demonstrated segregated social structure but broad spatial overlap when distribution was measured at the landscape scale of 0.25 km². Despite the broad overlap in use of space, males and females followed different strategies in the way space was used. During peak periods of segregation (June-October), male behaviors were consistent with a pre-rut energy saving and forage seeking strategy; males used larger areas and made longer short term movements than females, but were less active overall and spent relatively more of their active time during nocturnal periods than females. Females were less mobile and foraged in smaller areas than males, particularly during fawn rearing periods (June-October). Females used the same areas during peak segregation and the rut. Males, however, visited unfamiliar areas during the rut and were found to have a more ephemeral social structure than females. An explanation for the ephemeral congregation of males based on attraction to common resources and increased security is proposed.

Introduction

Sexual segregation has been hypothesized to occur among ungulates as the ultimate consequence of intersexual differences in energetic and reproductive strategies (Main and Coblentz, 1990). This hypothesis has been supported directly by recent studies of habitat partitioning in desert bighorn sheep (Ovis canadensis nelsoni; Bleich, 1993), Alaskan moose (Alces alces; Miquelle et al., 1992), and Rocky Mountain mule deer (Odocoileus hemionus hemionus; Main, 1994; Chapters 3 and 4). Additional evidence consistent with this hypothesis has primarily come from populations in heterogeneous environments, where spatial segregation was pronounced due to gender differences in habitat selectivity (Berger, 1991; Bergerud et al., 1984; Bowyer, 1984; Festa-Bianchet, 1988; Jakimchuk et al., 1987; Ordway and Krausman, 1986; Shank, 1982). In populations where females appear to use higher quality habitat or habitats with greater forage-producing potential, it has been suggested that males segregate in response to the competitive effects of female foraging pressure on preferred diet items (Clutton-Brock et al., 1987; Ilius and Gordon, 1987; Main and Coblentz, 1990).

Sexual segregation has also been reported for ungulate populations in habitats where resources were relatively evenly distributed. Although the Main and Coblentz (1990) hypothesis has been supported for woodland bison (Bison bison athabasca; Komers et al., 1993), and inferred as the probable impetus for black-tailed deer (O. h. columbianus; Weckerly, 1993), and white-tailed deer (O. virginianus; LaGory et al. 1991), it is seemingly not supported by studies of white-tailed deer from the George Reserve, Michigan, where it was concluded that males used poorer habitats and obtained diets of poorer quality than

females (Beier, 1987; Beier and McCullough, 1990; McCullough, 1979). Three hypotheses were proposed by these authors to explain segregation and the use of poorer quality habitat by males in this population. These were: 1) male avoidance of competition with offspring and potential offspring; 2) superior male ability to digest poor quality forage due to allometric relationships between body size, digestive capacity, and metabolic requirements; and, 3) male ranging behaviors and social organization designed to learn the distribution of potential breeding partners and establish pre-rut dominance relationships among potential rivals. The first hypothesis invokes altruism and is regarded as highly unlikely (Main and Coblentz, 1990). The second hypothesis lacks incentive. Although males may be more efficient than females at digesting poor quality forage, this fails to explain why they would choose poorer quality diets unless the energetic costs of obtaining sufficient amounts of forage from areas used by females was prohibitive, in which case this hypothesis is no different from that proposed by Main and Coblentz (1990). The last hypothesis, that segregation provides benefits in terms of familiarity with the distribution of potential mates and rivals has not been examined in detail.

The objectives of this study were to determine if 1) sexual segregation occurred in a population of white-tailed deer living in a relatively homogeneous environment in south Texas; 2) if patterns of sexual segregation were consistent with a "scouting" hypothesis based upon male familiarity with a) potential mates and b) potential rivals; and, 3) if sexual segregation was consistent with explanations based on the hypothesis that males and females segregate in response to different reproductive and energetic strategies.

Study Area

This study was conducted during January-December 1991 on approximately 2,400 ha of the 3,157 ha Rob and Bessie Welder Wildlife Foundation Refuge (WWR). The WWR is located in the south Texas Coastal Bend (ca. 28°06'N, 97°22'E) in a transitional zone between the Gulf Prairies and Marshes and the South Texas Plains (Gould, 1975).

The physical environment was relatively homogeneous; topography was flat (3-14 m), water was widely available, and vegetation was similar throughout the study area. Vegetation was dominated by two major communities, mesquite-mixed grass (ca. 41%) and chaparral-mixed grass (ca. 34%). Both communities had similar structural characteristics and were composed of many shared species (e.g., honey mesquite, Prosopis glandulosa; huisache, Acacia farnesiana; blackbrush acacia, A. rigidula). Detailed descriptions of the climate, geology and soils, vegetation, and animal life of the refuge are provided elsewhere (Box, 1961; Box and Chamrad, 1966; Box et al., 1979; Drawe et al., 1978). Annual precipitation is variable and periodic droughts occur (20 yr. $\bar{X}$ = 83.9 cm, SD = 31.6; unpubl. refuge records). Annual rainfall during this study was 112.6 cm, over double the annual average of the preceding 3 years ($\bar{X}$ = 52.1 cm, SD = 11.2).

White-tailed deer occurred throughout the study area. Based on the annual January helicopter survey, white-tailed deer occurred at densities of ca. 21.3 deer/km² during 1991 (unpubl. refuge records). Hunting is prohibited on the refuge and predators are protected. Coyotes are the primary deer predator and exert a significant influence on fawn mortality (Kie, 1977). There was no livestock grazing on the study area during 1990-1991.

Methods

Survey Information

Group composition, location, vegetation cover-type, and an index to density of woody vegetation were recorded for all deer groups ($n \geq 1$) observed during morning and evening surveys during January-December 1991. Seasonal periods were defined according to observed patterns of segregation, *i.e.*, the tendency for deer to form or avoid forming mixed-sex groups (Fig. V.1.), as these patterns corresponded with biologically meaningful periods. Seasonal periods were defined as: 1) January-February (post-rut, winter green-up), March-May (pre-parturition, availability of spring forage), June-October (parturition and fawn-rearing, summer forage, pre-rut), and November-December (rut, winter forage). Decisions to base analyses on monthly or seasonal periods varied with the appropriateness of the comparisons and available sample sizes.

Deer groups were identified as male, female, or mixed-sex by the presence of adult individuals. The universal transmercator (UTM) coordinate system (Grubb and Eakle, 1988) was used to map deer locations in 0.25 km^2 grid cells on 7.5 minute USGS topographic maps. Four cover-types were defined by combining similar communities previously mapped and described by Drawe et al. (1978). For example, two poorly represented communities, mesquite-bristlegrass and huisache-mixed grass, were pooled with mesquite-mixed grass which covered approximately 41% of the study area. Pooling communities was justified on the basis of similar structure and species composition, and because poorly represented communities comprised <10% of the study area. Percent cover for defined cover-types was

estimated from maps in Drawe et al. (1978) as: 1) mesquite-mixed grass (MESQ, 43%), 2) chaparral-mixed grass (CHAP, 37%), 3) bunchgrass-annual forb (BG-AF, 19%), and 4) closed-canopy woodlands (CC, 1%). The density of woody vegetation at locations where deer groups were observed was estimated according to methods used by Hirth (1977). Three density categories were recognized: 1) open (<10% cover), 2) intermediate (10-60% cover), and dense (>60% cover).

Statistical analyses of survey data used deer groups as the statistical unit to avoid violating assumptions of independence. The only exceptions to this were the use of Schoener's (1968, 1970) overlap index, a measure of spatial overlap between males and females (refer to Chapter 4 for detailed description) and Spearman rank correlation coefficients (Sokal and Rohlf, 1981). Both of these analyses were applied to total individuals rather than groups to examine the influence of total deer observed in 0.25 km² cells on the presence/absence of the opposite sex (McCullough et al., 1989). Because significance tests are not available for overlap indices, sex differences in spatial distribution were also examined with G-tests by comparing the number of shared versus exclusively used 0.25 km² cells containing ≥ 3 group observations of either sex (Main, 1994; Miquelle et al., 1992). Comparisons of mixed versus segregated groups, the use of cover-types by sex, and the density of woody vegetation at observation sites were analyzed with G-tests (Sokal and Rohlf, 1981) and used deer groups as the statistical unit.

Radiotelemetry Information

A helicopter and drive nets were used to capture 8 adult (≥ 2.5 yr.) males and 8 adult females throughout the study area. Captured deer were not sedated but an assisting veterinarian provided each animal with a broad spectrum antibiotic (Liquamycin^R LA-200, 10 mg/kg), an anti-inflammatory corticosteroid (Dexamethasone^R, 2 mg), and a selenium-vitamin E mixture (BO-SE^R; 1 mg and 50 mg, respectively) to prevent stress-induced myopathy. Deer were equipped with coded ear-tags and radio-transmitters with activity sensors (Telonics^R, Inc.). Male collars differed from those of females only in that they were dyed hunter orange and were expandable.

Locations of radio-collared deer were obtained during regular morning (0500-0900 h), diurnal (1000-1600 h), evening (1700-2100 h), and nocturnal (2200-0400 h) periods by triangulation with a hand-held Telonics^R H-antenna and portable receiver (bearings/location: $\bar{X} = 2.9$, $SD = 1.4$, $n = 750$ random samples), and by opportunistic sightings. Schedules were arranged such that morning and evening locations would be obtained one day and diurnal and nocturnal locations the next or vice versa, with an 8 hour minimum between consecutive locations. This was assumed to be sufficient for independence of consecutive observations; Weckerly (1993) concluded 3 hour intervals were sufficient for consecutive black-tailed deer locations. Schedules and route patterns were varied to randomize the order in which individuals were located.

Triangulation accuracy was enhanced by flat topography, an extensive network of roads and pipelines which promoted proximity to radio-collared individuals (bearing distance: $\bar{X} = 323$ m, $SD = 138$, $n = 500$ random samples), and the establishment of approximately 150

permanent locations that increased triangulation efficiency (triangulation time: $\bar{X} = 9.1$ mins./loc., $SD = 2.9$, $n = 750$ random samples). Bearing accuracy (absolute $\bar{X}$ error = 2.23° , $SE = 3.34$), bias ($\bar{X} = -0.26$), and precision ($SD = 0.39$) were estimated by methods of Lee et al. (1985) and based on ten replicate bearings obtained from ≥ 2 stations for each of 8 transmitter locations throughout the study area (test distance: $\bar{X} = 557$ m, $SD = 227$).

Bearings were inspected and plotted with XYLOG^R (Dodge and Steiner, 1986), and all locations were recorded in UTM mapping coordinates. Home ranges were calculated by minimum convex polygon (Mohr, 1947) and harmonic mean (Dixon and Chapman, 1980) methods using the McPaal^R home range program (Stuwe and Blohowiak, 1985). Average monthly home range was compared between sexes by ANOVA using log transformed data to correct for departures from normality. Home range estimates produced by MCP and harmonic mean methods were compared both with ANOVA and graphically to determine if similar monthly patterns were produced. McPaal^R was also used to map locations in 0.25 km^2 cells for comparisons of areas (cells) used during June-September with areas used during November-December. Comparisons were made both among individuals within sexes (G -test for heterogeneity, G_H) and between periods with a replicated goodness of fit G -test, G_r (Sokal and Rohlf, 1981). Diurnal movements were calculated as the linear distance between successive morning (0500-0900 h) and evening (1700-2100 h) locations. Nocturnal movement distances were similarly calculated between evening and morning locations. Movement data were log transformed and simultaneously analyzed among sex, seasons, and time with ANOVA.

Activity data was obtained from pulse changes mediated by activity sensors. Active "scores" were assigned if active pulse frequencies were maintained continuously for ≥ 10 seconds or sporadically for shorter periods when collecting bearings. Individuals were classified as active if $\geq 50\%$ of two or more bearings received active scores. Activity data were analyzed within sexes and between sexes by time period (as above) and season with two-way contingency tables (Statgraphics^R). In addition to opportunistic sightings, radio-collared deer were located during mid-day with the help of an assistant at least once each week to visually assess group compositions. Only those observational data with a reasonably good expectation of being accurate (e.g., deer observed in clearings or from towers) were used. Group composition data was used to evaluate gender differences in social group stability. Social stability was measured as the average variation (Sokal and Rohlf, 1981:182), or the average rate of change, in group composition among successive observations. This approach was preferred over simply measuring the variation in average group size because this could be influenced by relatively few observations and would tend to be greater for the sex with the larger average group size. Only adults of the same sex were used in calculations of social stability because mixed-sex groups were infrequent and would be inappropriate for measuring the stability of social structure by gender. Yearlings and fawns were also excluded because I was interested in relationships among adult deer, and fawns were much less visible than adults which would artificially bias the variability of female groups. Statistical comparisons in social group variability were made between sexes by month with a series

of F-tests after weighting average variations by sample size (Sokal and Rohlf, 1981:190).

Results

Sexual segregation was pronounced at WWR, (90% of 1,778 deer groups observed were single-sex) and varied significantly among months ($\underline{G} = 74.11$, $\underline{P} < 0.001$; Fig. V.1.). Although the sexes segregated socially, there was no evidence that males and females used different areas at a landscape scale of 0.25 km² when measured by Schoener's (1968) overlap index or Spearman rank correlation (Table V.1.), or by an analysis of cells used by both sexes versus cells used exclusively by one sex ($\underline{G} = 84.8$, $\underline{P} < 0.001$).

Table V.1. Spatial overlap among males and females based on observations within 0.25 km² cells during 4 seasonal time periods. Overlap measured by Schoener's (1968) overlap index ($\underline{C}$) and Spearman rank correlation coefficients ($\underline{R}_s$, with P-values).

<u>Period</u>	<u>Total Males</u>	<u>Total Females</u>	<u>Total Cells</u>	Schoener	Spearman Rank	
				Index <u>C</u>	Correlation <u>r_s</u>	<u>P</u>
Jan.-Feb.	125	450	20	0.75	0.76	<0.001
Mar.-May	132	246	23	0.63	0.003	0.989
June-Oct.	453	1,051	45	0.67	0.55	<0.001
Nov.-Dec.	143	341	29	0.70	0.52	0.006

In addition to broad spatial overlap, males and females used vegetative cover-types similarly ($\underline{G} = 1.45$, $\underline{P} > 0.90$). However, mixed-sex groups used cover-types significantly different from male ($\underline{G} = 7.48$, $\underline{P} < 0.10$) and female groups ($\underline{G} = 8.91$, $\underline{P} < 0.05$) due to the occurrence of large, mixed-sex feeding aggregations in BG-AF communities during January-February (Table V.2.). Cover-type use varied seasonally (Fig. V.2.) and followed similar seasonal patterns among all group-types (Table

V.2.). Although males and females used the same cover-types, male groups were observed in denser woody vegetation (Fig. V.3.) significantly more often than female groups ($\bar{G} = 8.45$, $P < 0.01$) or mixed-sex groups ($\bar{G} = 8.22$, $P < 0.10$). Female and mixed-sex groups were observed in similar densities of woody vegetation ($\bar{G} = 1.63$, $P > 0.75$). Seasonal patterns in the density of shrubby vegetation at observation sites were broadly similar among group-types, with open areas being used significantly more in March-May ($\bar{G} = 32.62$, $P < 0.001$) and heavier cover being used progressively more during June-October and November-December. Although no visibility data were collected during January-February, deer were commonly seen in open BG-AF communities (Fig. V.2.) during this period.

Table V.2. Percent observations of male, female, and mixed-sex groups by vegetative cover-types during 4 seasonal time periods. Sample sizes (deer groups) are provided in parentheses. Woodland cover-types omitted because observed use was $< 5\%$ at any time.

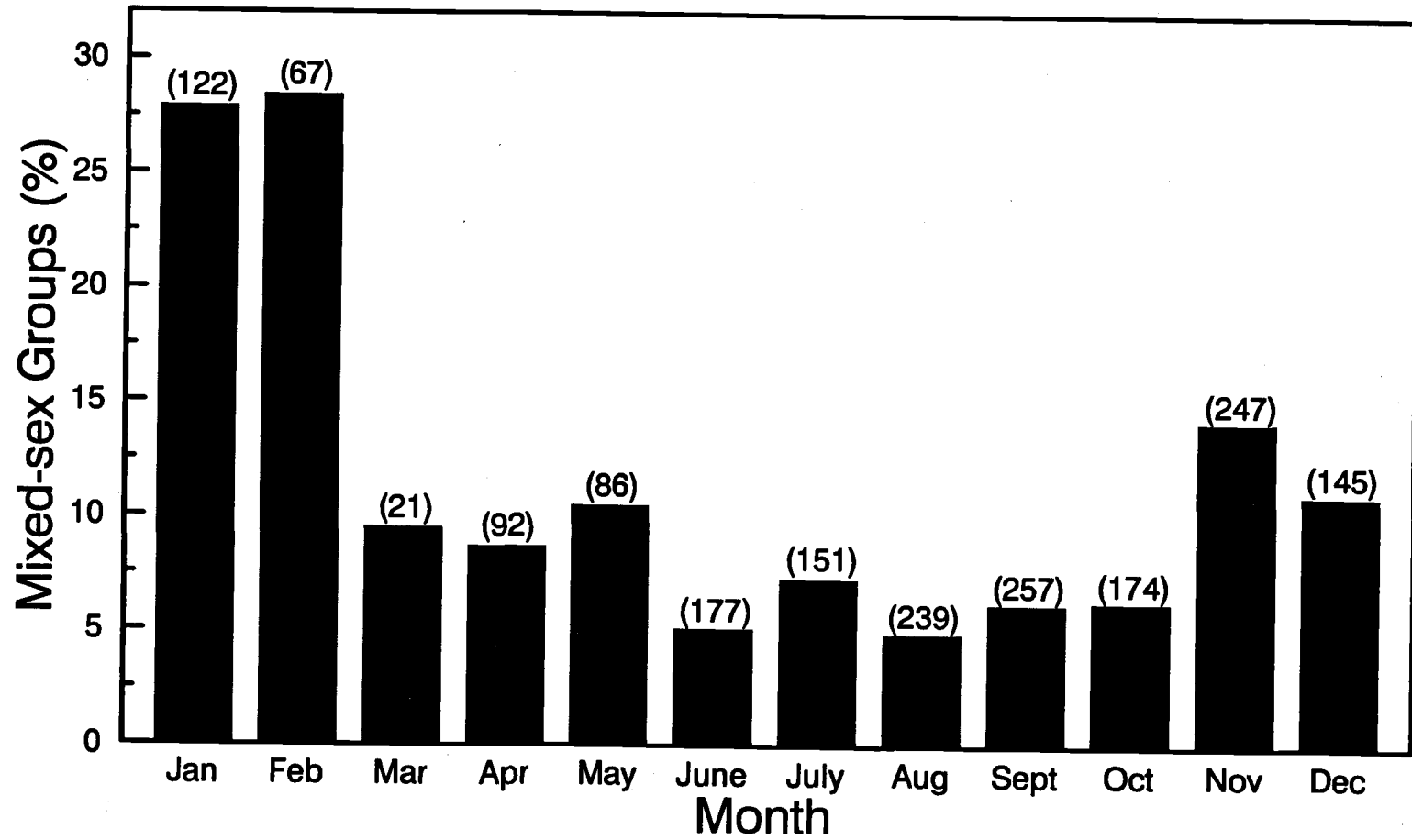
<u>Period</u>	<u>Group-type</u>	<u>Bunchgrass- Annual forb</u>	<u>Chaparral- Mixed grass</u>	<u>Mesquite- Mixed grass</u>
Jan.-Feb.	Male	43% (17)	38% (15)	20% (8)
	Female	37% (35)	28% (27)	35% (33)
	Mixed	55% (29)	23% (12)	23% (12)
Mar.-May	Male	25% (15)	25% (15)	50% (31)
	Female	20% (23)	24% (27)	56% (63)
	Mixed	11% (2)	39% (7)	50% (9)
June-Oct.	Male	14% (27)	46% (91)	40% (78)
	Female	11% (65)	36% (217)	53% (321)
	Mixed	12% (7)	30% (18)	58% (35)
Nov.-Dec.	Male	14% (11)	40% (32)	47% (38)
	Female	12% (21)	35% (63)	53% (94)
	Mixed	06% (3)	38% (19)	56% (28)

Figure V.1. Percentage of deer groups observed containing ≥ 1 adult member of each sex by month. Sample sizes provided in parentheses.

Figure V.2. Percent use of bunchgrass-annual forb (BG-AF), chaparral (CHAP), and mesquite (MESQ) cover-types by seasonal period. Male, female, and mixed-sex group-types followed similar seasonal patterns and are pooled. Sample sizes (deer groups) provided in parentheses.

Figure V.3. Percentage of male, female, and mixed-sex group observations in each of three cover classifications for horizontal woody vegetation. Sample sizes (deer groups) provided in parentheses.

Figure V.1.



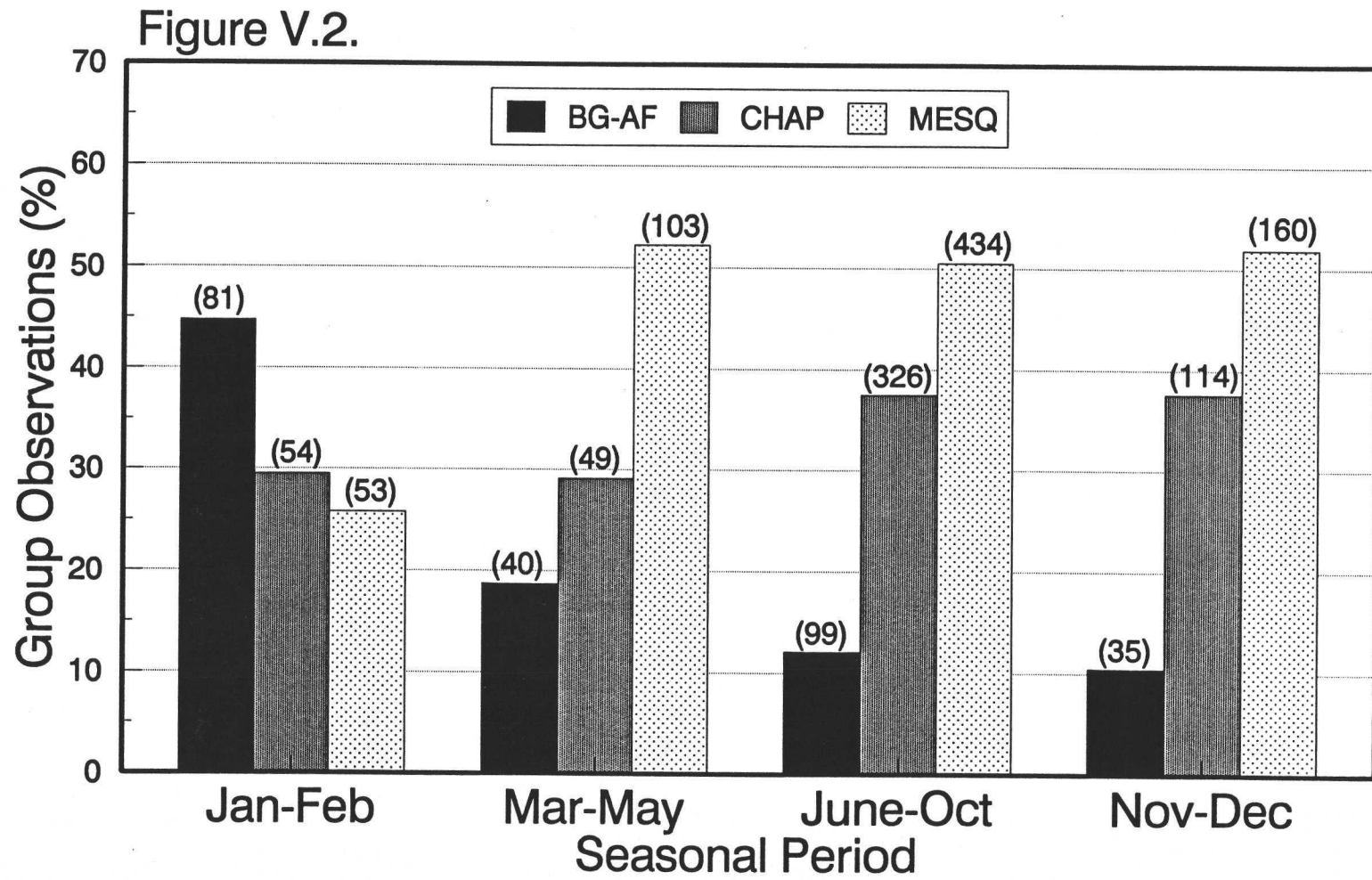
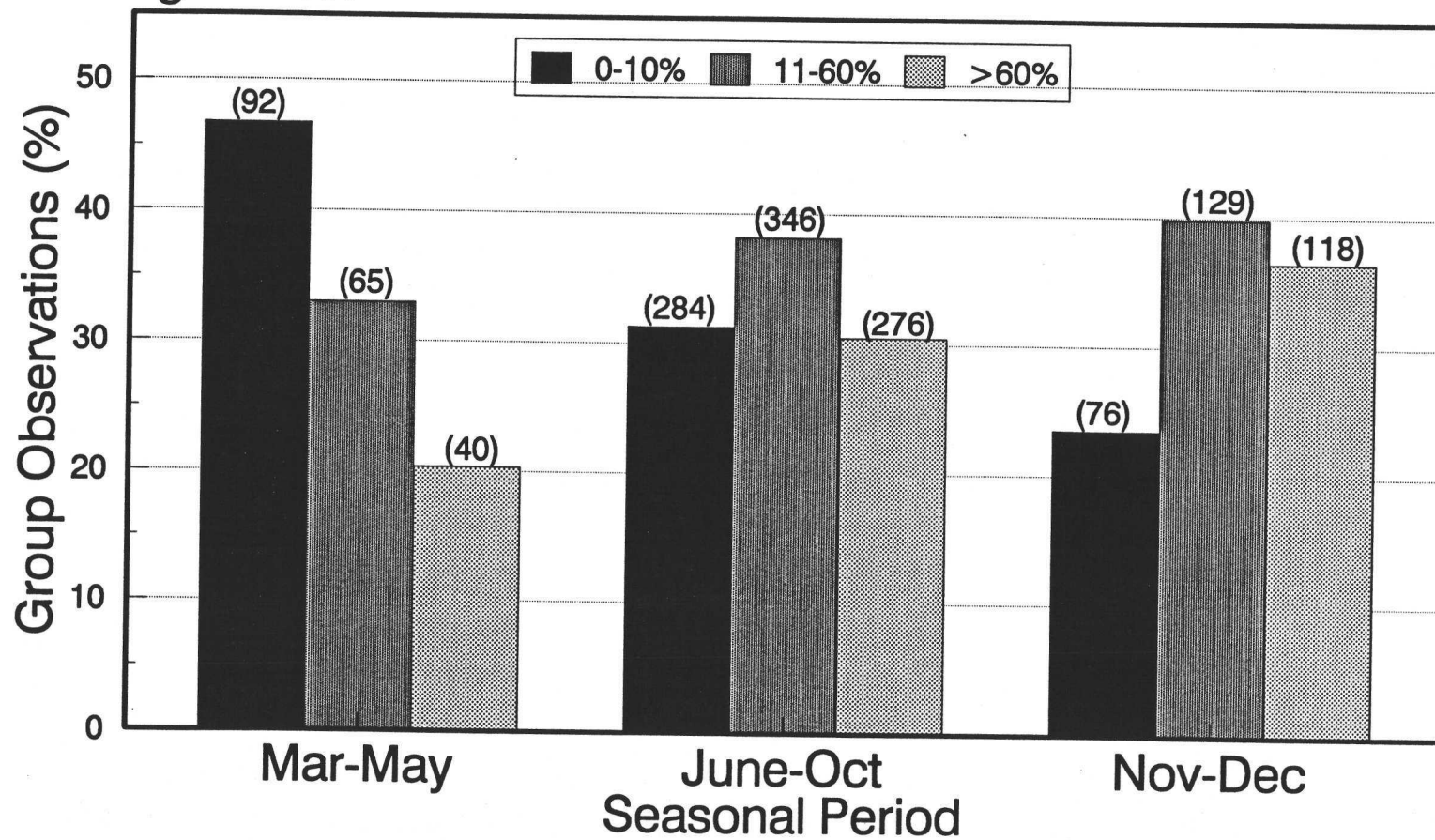


Figure V.3.



Radio-collared deer were relocated 3,957 times ($\bar{X}$ = 26.7 locations/deer/month, SD = 4.0) during January-December. Average home ranges were significantly larger ($P < 0.001$) for males than females when calculated by either MCP or 95% harmonic mean methods. Overall, 95% harmonic mean estimates were significantly larger than those generated by MCP ($F = 6.07$, $P = 0.01$), but both methods provided similar patterns that revealed males used larger areas during every month (Fig. V.4.).

Males were also more mobile than females in the short term and traveled significantly greater distances between locations over 8-12 h diurnal and nocturnal periods during March-December (Fig. V.5.). During the rut (November-December), males expanded home ranges into areas where they were never located during peak (June-September) periods of segregation despite the greater numbers of locations (J-S: $\bar{X}$ = 108.3, SD = 5.4; N-D: $\bar{X}$ = 33.2, SD = 0.4) and larger overall areas used (J-S: $\bar{X}$ = 3.45 km², SD = 2.02; N-D: $\bar{X}$ = 2.85 km², SD = 0.38) during the June-September period. October was excluded because the objective was to compare areas used during breeding and non-breeding periods, and pre-rut behavioral changes associated with hormonal changes in October might confound results. During the rut, males were re-located in 0.25 km² cells visited during June-September an average of 60.6% (SD = 33.3) of the time. Although responses varied among individual males ($G_H = 106.6$, $P < 0.001$), males used previously visited areas significantly less than expected based upon an arbitrary and conservative expected overlap of 75% ($G_T = 124.8$, $P < 0.001$). While males spent a considerable time in unfamiliar areas during November-December, females did not. On average, females were observed in the same 0.25 km² cells used during June-September 96% of the time and several females were re-

located in previously used cells exclusively. With the exception of one female that made repeated trips to a cultivated field of sorghum (*Syricum* spp.), females behaved similarly ($G_H = 8.34$, $P > 0.10$). Female home ranges did not differ between the June-September and November-December periods even when expected overlap was increased to 95% ($G_T = 8.57$, $P > 0.10$).

Although males made longer movements and used larger home ranges, they were significantly less active than females during every season ($P < 0.01$), except January-February when activity levels were similar between sexes ($\chi^2 = 0.40$, $P = 0.53$). Overall, the percentage of active females was higher during morning ($\chi^2 = 52.4$, $P < 0.0001$), mid-day ($\chi^2 = 26.8$, $P < 0.0001$), and evening periods ($\chi^2 = 35.8$, $P < 0.0001$), and similar to males during nocturnal periods ($\chi^2 = 0.16$, $P > 0.98$; no nocturnal information available from November-December). Intrasexually, females were significantly more active during morning and evening periods than during mid-day and nocturnal periods ($\chi^2 = 45.84$, $P < 0.0001$). Although male activity levels also peaked during evening and morning, activity levels during nocturnal periods were similar to morning and significantly higher than at mid-day ($\chi^2 = 17.99$, $P < 0.0001$). Intersexual differences in activity patterns were most pronounced during June-October when males maximized nocturnal and minimized diurnal activity (Table V.3.).

Fluctuations in the number of same-sex adults observed with radio-collared individuals during successive observations (i.e., social group stability) varied seasonally between males and females (Fig. V.6.), as did average group sizes observed during surveys (Table V.4.). Group compositions fluctuated significantly more among females during pre-rut (October; $F = 5.05$, $P < 0.001$) and

post-rut (January-February; $F = 2.67$, $P < 0.001$) periods, while male groups fluctuated more during spring through summer (April-August; $P < 0.01$, all months). Fluctuations in group composition were similar ($P > 0.10$) between the sexes during March, September, and November-December. Although male groups fluctuated more than those of females during much of the year, males were also solitary a great deal. Survey records of 579 deer groups with ≥ 1 adult male revealed that males were solitary 46% of the time during non-reproductive periods (January-September), and that solitary behavior increased sharply during October (84%) and November-December (83%).

Table V.3. Comparison of male and female activity levels during June-October, recorded as the percentage of radio-collared individuals active during morning (0500-0900 h), diurnal (1000-1600 h), evening (17-21 h), and nocturnal (22-4 h) periods.

Period	Sex	n	Active (%)	Sex Comparisons	
				χ^2	P
Morning	Male	333	54.4	42.67	<0.0001
	Female	346	78.0		
Diurnal	Male	188	26.1	18.00	<0.0001
	Female	196	46.9		
Evening	Male	345	57.7	29.36	<0.0001
	Female	376	76.6		
Nocturnal	Male	60	58.3	0.25	0.62
	Female	54	53.7		

Table V.4. Average group sizes for male, female, and mixed-sex groups during 4 seasonal time periods. Standard deviations provided in parentheses.

Period	Male groups		Female groups		Mixed groups	
Jan.-Feb.	2.24	(1.79)	4.01	(2.20)	9.79	(9.38)
Mar.-May	2.30	(1.41)	3.07	(1.03)	5.42	(2.80)
June-Oct.	2.08	(1.32)	1.85	(1.09)	4.58	(2.30)
Nov.-Dec.	1.28	(0.60)	1.73	(1.07)	2.98	(1.35)

Figure V.4. Mean home range and standard deviation for radio-collared males and females by month (calculated by minimum convex polygon). January-February (JF) and November-December (ND) pooled. Total number of transmitting collars/month provided in parentheses.

Figure V.5. Mean distance (with standard errors) moved by radio-collared males and females between morning (0500-0900 h) and evening (1700-2100 h) locations (= diurnal movements) and between evening and morning locations (= nocturnal movements), by seasonal period. Total movements provided in parentheses.

Figure V.6. Social group stability measured as the average variation in the number of same-sex adults observed with radio-collared males and females during successive observations, by month (Sokal and Rohlf, 1981:182). January-February (JF) and November-December (ND) pooled. Total visual records provided in parentheses.

Figure V.4.

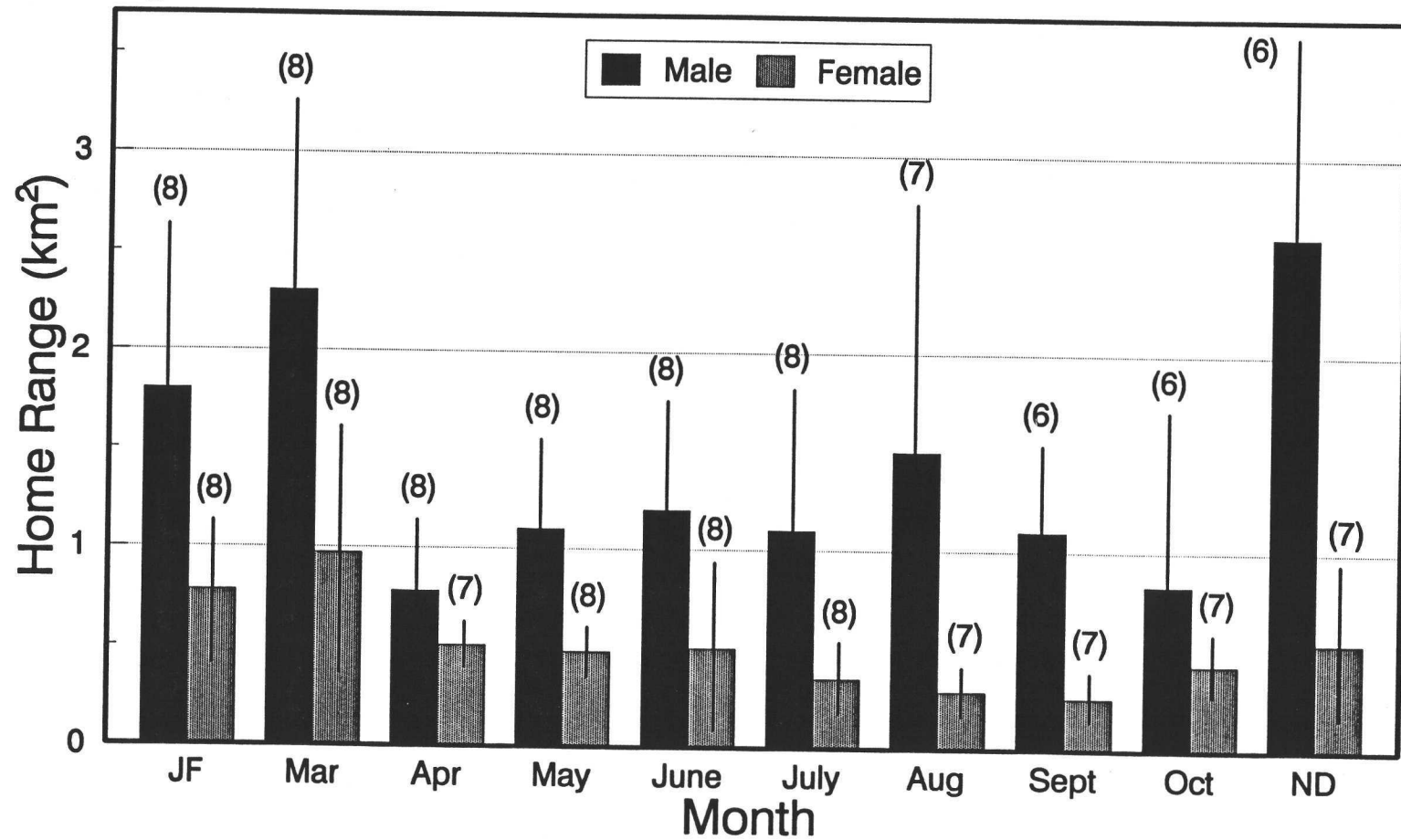


Figure V.5.

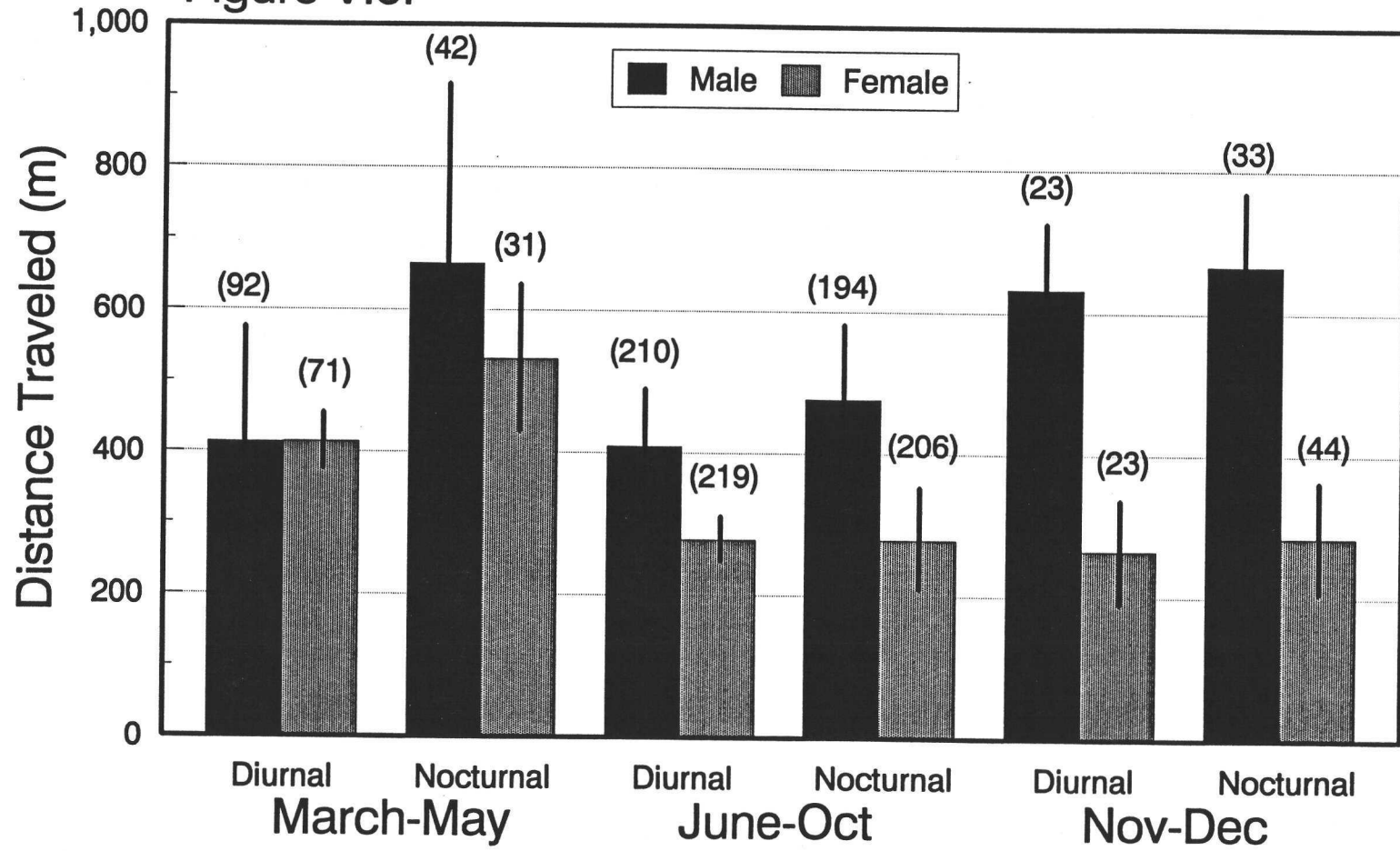
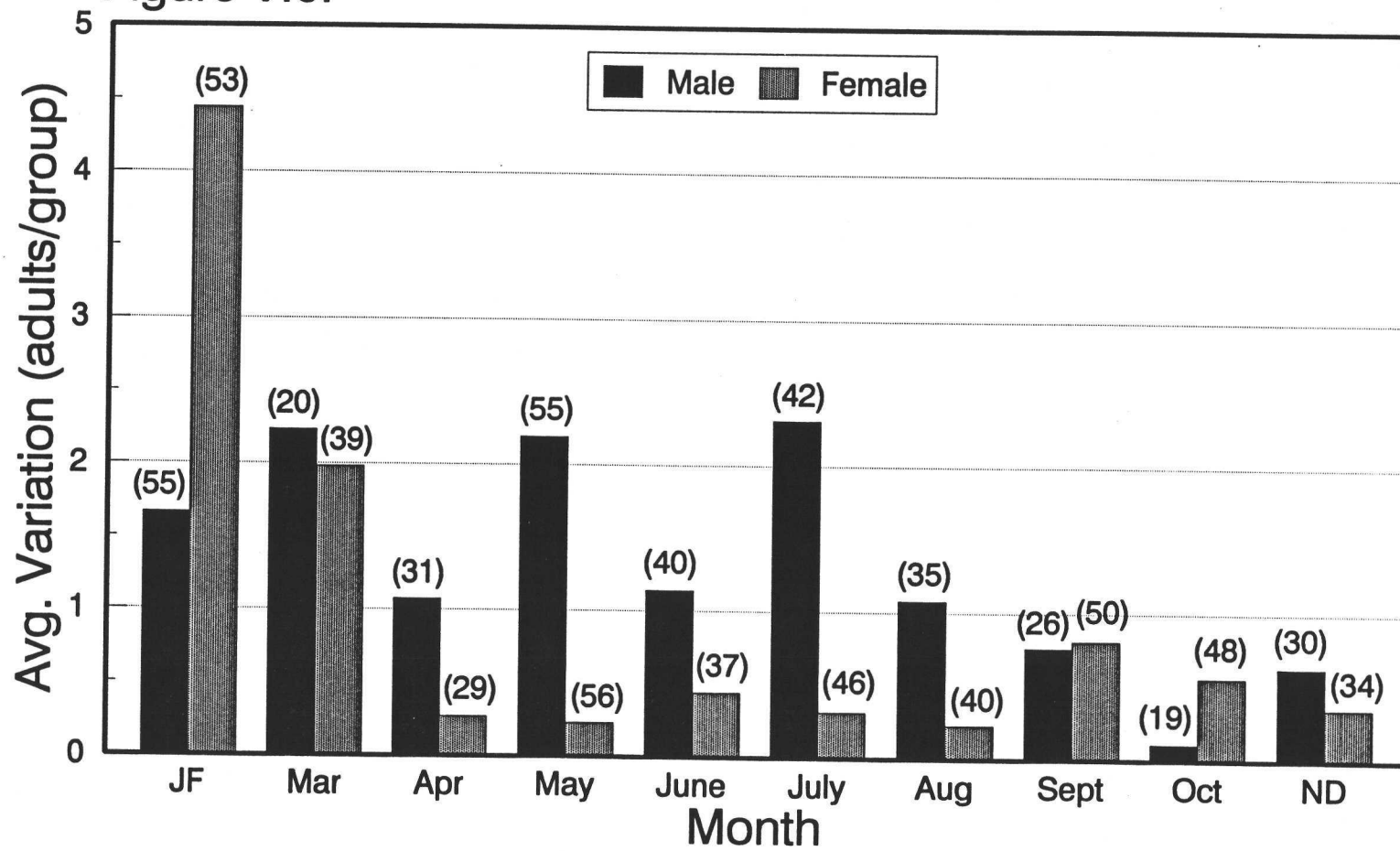


Figure V.6.



Discussion

Male and female white-tailed deer segregated into separate social groups but used the same general areas (Table V.1.) and similar cover-types (Fig. V.2.) when spatial distribution was measured at a scale of 0.25 km^2 at WWR. These results were not surprising when the high density of deer (21 deer/km^2 ; unpubl. refuge records), widespread availability of requisite resources, and ubiquitous distribution of female groups was considered. In short, there was virtually no place males could go without also overlapping areas also used by female groups since males used much larger home ranges than females (Fig. V.4.). The 0.25 km^2 scale used to measure spatial distribution may have been inadequate to detect fine scale differences as reported by McCullough et al. (1989) for white-tailed deer on the George Reserve, Michigan. Fine scale differences in resource partitioning may have existed at WWR, suggested in part by pronounced segregation of males and females into separate social groups (Fig. V.1.) and by differences observed in the density of woody vegetation at observation sites (Fig. V.3.)

Observed seasonal patterns of social segregation corresponded to reproductive patterns and forage availability. While mixing during November-December was related to breeding activity, the increased occurrence of large mixed-sex groups during January-February and, to a lesser extent during March-May (Fig. V.1., Table V.4.), represented feeding assemblages responding to emerging grasses and forbs, particularly in the open BG-AF and MESQ cover-types (Chamrad and Box, 1968). When emergent forbs and grasses became widely available fawns were approaching one year of age and likely did not restrict the behavior

of females, as evidenced by the increased home range (Fig. V.4.), group size (Table V.4.), and variation in composition (Fig. V.6.) of female groups during this period.

As predicted by Main and Coblentz (1990), social segregation was most pronounced during the period when behavioral strategies related to reproductive success differed most between males and females, i.e., during June-October when females were restricted by maternal obligations and males were attempting to maximize pre-rut energy reserves. In addition to fawns restricting female home range size directly (Fig. V.4.; McCullough et al., 1989), increased aggressiveness and the establishment of social barriers by females with fawns probably also restricted mobility of other females (Fig. V.6.; Hirth, 1977; Geist 1981; Ozoga et al., 1982; Schwede et al., 1993). Males, on the other hand, used larger home ranges (Fig. V.4.) and traveled greater distances between locations (Fig. V.5.) than females during this period, a strategy that may enable them to circumvent the effects of localized female foraging pressure (Clutton-Brock et al., 1987; Main, 1994; Chapter 4).

Larger male movements and home ranges during spring and summer was also consistent with a "scouting" hypothesis (Beier and McCullough, 1990; McCullough, 1979), in which males segregate and use larger home ranges prior to the rut in order to obtain information about potential mates and rivals. Average variation in group composition (Fig. V.6.) was much higher for males than females during February-August and also appeared to support both hypotheses. Males may have formed ephemeral groups as a means to assess the status of potential rivals or may have simply been attracted to common resources and formed temporal associations for selfish reasons (Hamilton,

1971). Female group composition varied the least during the last trimester of pregnancy through the first 3 months postpartum. This pattern corresponds with the small, stable matrilineal groups observed during April-May and the aggressive behavioral patterns that increased postpartum, a strategy that may be important for reducing the depletion of resources in small home ranges (Geist, 1981) and minimizing disturbance to fawns (McCullough, 1979; Ozoga et al., 1982). Although male movements, home range size, and ephemeral social structures were consistent with either explanation, evidence inconsistent with the scouting hypothesis suggested that scouting of mates and rivals was not the primary impetus for segregation by males.

Activity data was supportive of the energetic/reproductive hypothesis but inconclusive for the scouting hypothesis. Females were more active than males during all seasonal periods except January-February, and during all but nocturnal time periods. This suggests that females spent more time and expended more energy than males finding food, while minimizing nocturnal activity when the ability to detect predators was reduced. Additionally, sex differences were most pronounced during June-October when males minimized diurnal activity (Table V.3.). While minimizing diurnal activity would be energetically efficient, from the perspective of effectively scouting prospective mates it would seem that male activity peaks should coincide with those of females.

The most convincing evidence against the scouting hypothesis was that during the rut, roughly 40% of the locations for radio-collared males were in areas never used during June-September despite the greater numbers of locations and the larger combined home range used during June-September. If males segregated to learn the

distribution of potential mates, then males should attempt to breed in areas scouted, particularly since females did not shift home ranges. Males, therefore, spent considerable effort searching for mates in unscouted territory. While males could conceivably benefit from learning the distribution of potential breeding partners, male search patterns outside of their normal range during the rut suggested this was not important. Additionally, the expansion of home ranges (Fig. V.4.) and the use of unfamiliar areas during November-December would increase the likelihood of encountering males of unknown status and time and energy requirements to resolve that status. Although it is conceivable that males may derive benefits from previously established hierarchical relationships, this may not be of paramount importance because aggressive behavior is highly ritualized and only infrequently results in serious injury (Geist, 1981; Marchinton and Hirth, 1984). Additionally, Clutton-Brock et al. (1988) found no consistent relationship between dominance status of red deer bulls while in bachelor groups and their fighting ability and mating success during the rut. Brown (1974) also reported a reversal in summer dominance status between two similarly sized white-tailed bucks during the rut. In short, dominance relationships developed during ephemeral male social gatherings are likely unimportant relative to contests over mates because the motivational factors are enormously different. Additional compelling evidence against the argument that males segregate and use larger home ranges to scout potential mates and rivals is provided by the numerous examples where males segregate to areas where females are rare or nonexistent (see reviews in Bleich, 1993; Main and Coblentz, 1990; Miquelle et al., 1992). In these situations, learning the distribution of potential breeding partners cannot be invoked, nor is it

likely that males on a given summer range would be the only individuals encountered during the breeding period because males from different areas may be attracted to the same females.

Male use of unfamiliar areas during the rut (November-December) was not, however, inconsistent with the hypothesis that sexual segregation occurred as the result of different energetic and reproductive strategies between the sexes. The larger home ranges, longer movements, and energy conserving behavior of males was consistent with an optimal foraging strategy that would decrease foraging pressure in any given area and increase utilization of new forage patches (Bunnell and Gillingham, 1985; Charnov, 1976). This would be especially true if sexual segregation resulted in resource partitioning and differences in spatial foraging patterns, albeit at a fine scale, as reported by McCullough et al. (1989). If the impetus for segregation was primarily related to obtaining information on mates and rivals, males would be expected to breed in the same areas occupied during peak periods of segregation.

If sexual segregation provides benefits to males by increasing foraging opportunities in a relatively homogeneous environment, it seems that this must occur primarily from a reduction in competition with females for preferred diet items (Selander, 1966), rather than other social factors such as avoidance of intersexual aggression, because adult males are dominant to females (Hirth, 1977; pers. observ.). The potential for competitive interactions exists because diets are similar between the sexes. A review of deer diet studies at WWR over a 12 year period revealed that deer primarily consumed forbs which typically constituted between 70-90% of diets depending upon the season (Chamrad et al., 1979).

Kie et al. (1980) determined that adult males and females at WWR had similar diets predominated by forbs, and that no differences existed in rumen protein, phosphorus, or calcium contents. Additionally, it was determined that density-dependent effects negatively affected both sexes at WWR (Kie and White, 1985; Kie et al. 1979, 1980). Main (1994; Chapter 4) suggested female mule deer competitively excluded males from mesic habitats in a semi-arid environment and Clutton-Brock et al. (1987) suggested female red deer (Cervus elaphus) competitively excluded males from greens (meadows). The ubiquitous distribution of females and the lack of evidence indicating clear differences in spatial distribution at WWR suggested that, although females did not exclude males from using overlapping areas, they likely influenced male patterns of habitat use and probably also the condition of males as suggested by Kie and White (1985), who reported that mature males suffered higher rates of mortality at WWR when deer population densities were high.

On a speculative note, qualitative observations suggested that, especially during peak periods of segregation (June-October), males at WWR used large areas that overlapped female home ranges but generally avoided female core-activity areas. In effect, it appeared as though males concentrated feeding activity in the buffer zones between areas of greatest female activity, analogous perhaps to Mech's (1977) description of deer activity in buffer zones between wolf (Canis lupus) territories. To effectively test this hypothesis, spatial use patterns of all female groups and all males in a common area would need to be examined, which was not possible during this study. However, radiotelemetry locations during June-September from three males with home ranges that overlapped those of two radio-collared females were

suggestive. Total observations for these males in six 0.25 km² cells that contained 87.3% of the female observations averaged only 14.7% (SD = 7.4), a value that would almost certainly decrease at a finer scale of resolution.

The occurrence of sexual segregation at WWR was consistent with hypotheses that males and females exhibit different behavioral patterns related to reproductive fitness; males maximized pre-rut energy reserves, females maximized offspring security through localized behavioral patterns in suitable habitat. Because resources and female groups were homogeneously distributed, observed patterns of segregation lacked the distinct spatial component reported from heterogeneous environments, but were still consistent with arguments that segregation patterns by males were a response to foraging opportunities. Conservative management strategies designed to maintain high female densities may exacerbate these competitive interactions and eventually result in negative density-dependent effects that tend to operate disproportionately on fawns (Clutton-Brock et al., 1985; McCullough, 1984; McCullough et al., 1989; Teer, 1984), yearling males (Clutton-Brock, 1991; Clutton-Brock et al., 1982; Hines, 1975) and mature males (Clutton-Brock et al., 1982; Kie and White, 1985). These findings suggest that conservative female harvest strategies may be inconsistent with management objectives designed to recruit new males into the population and reduce mature male mortality unrelated to hunter harvest.

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